ICES Journal of
Marine Science
Journal du Conseil
Volume 71 Number 8 October 2014
http://icesjms.oxfordjournals.org/

Fluctuations in the great fisheries of northern Europe – Commemorating 100 years since Hjort's 1914 treatise

A special issue of the ICES Journal of Marine Science

ICES
CIEM
OXFORD
UNIVERSITY PRESS

ICES Journal of Marine Science

Journal du Conseil

Volume 71 Number 8 October 2014

http://icesjms.oxfordjournals.org/

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Published by Oxford University Press for
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer
H. C. Andersens Boulevard 44-46, DK-1553 Copenhagen V, Denmark

ICES Journal of Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 1989–1992. doi:10.1093/icesjms/fsu159

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Introduction

Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe: where we have been, where we are, and where we are going

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Browman, H. I. Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe: where we have been, where we are, and where we are going. – ICES Journal of Marine Science, 71: 1989–1992.

Received 15 August 2014; accepted 18 August 2014

The year 2014 marks the 100th anniversary of Johan Hjort's seminal treatise, *Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research*. This special issue of the *ICES Journal of Marine Science* commemorates this anniversary. The thirty-two articles that appear herein demonstrate the deep influence that Johan Hjort's work has had, and continues to have, on fisheries and marine science.

Keywords: climate change, density dependence, settlement, Johan Hjort, juveniles, larvae, migration hypothesis, recruitment variability, stock–recruit; critical periods.

Background

The year 2014 marks the 100th anniversary of Johan Hjort's seminal treatise, *Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research* (Hjort, 1914). Since this and many other works by Hjort appeared in the pages of ICES publications, including the precursor of this journal, it seemed natural to commemorate this anniversary in the *ICES Journal of Marine Science*. Therefore, in mid-2012, I distributed a call for contributions to this special issue. My hope was that the entire fisheries science community would be able to produce a special issue with more pages than Hjort's treatise (228), even in this era of the minimum publishable unit and the enormous pressure on scientists to publish anything slightly more than that in a "high impact" journal. Thirty-two of the articles that were submitted in response to the call appear in this special issue—they total considerably more than 228 pages. These articles demonstrate the deep influence that Johan Hjort's work has had, and continues to have, on fisheries and marine science (also see Houde, 2008). In this introduction, I briefly summarize these articles, categorizing them into those that touch upon where we have been, where we are, and where we are going.

Where we have been

One hundred years ago, Johan Hjort distilled a large number of observations, and some of the first time-series of their kind (e.g. the age structure of individuals in a population and their condition), and posited a set of hypotheses that have driven fisheries science ever since (see Hjort, 1914, p. 209, under the heading, "Importance of future investigations as to the-causes of numerical variation"). The historical context in which Hjort accomplished this, and insights into the man and his work environment, is described by Schwach (2014). Hubbard (2014) provides insights into Hjort's activity on the eastern seaboard of North America and how this transformed fisheries science in Canada and established the still strong links between Canadian and Norwegian fisheries science. Holt (2014) provides fascinating insight into the scientific background and the interactions with contemporary researchers who influenced Hjort's thinking about the optimum yield. Aksnes and Browman (2014) present a bibliometric analysis of Hjort's work, concluding that the large number of citations that it has accrued, and the 40–50 citations that it continues to receive every year are exceptional for a 100-year-old scientific article and reflect its place as a seminal, novel, and paradigm-setting study that continues to drive fisheries science to this day.

Where we are

Several articles take up the questions addressed by Hjort (1914), sometimes using new innovations in sampling and analysis, application of mathematical models, adding climate change as a context, or with a slightly new "spin".

Leaf and Friedland (2014) explore the relationship between autumn phytoplankton bloom and recruitment variability of haddock (*Melanogrammus aeglefinus*) on the Georges Bank, concluding that the former has some explanatory power over the latter. Lusseau *et al.* (2014) conclude that recruitment failure in North Sea herring (*Clupea harengus*) is associated with poor feeding success. Robert *et al.* (2014) highlight the limits in our ability to identify the gut content of fish larvae as a possible reason why we have been unable to observe critical periods, as postulated by Hjort (1914, 1926): "As factors, or rather events which might be expected to determine the numerical value of a new year-class, I drew attention to the following two possibilities: 1) That those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. That in other words the origin of a rich year class would require the contemporary hatching of the eggs and the development of the special sort of plants or nauplii which the newly hatched larva needed for its nourishment." (Hjort, 1926, p. 33).

Hjort recognized the importance of the liver as an indicator of condition in cod (*Gadus morhua*) (Hjort, 1914, "Variations in the quality of the cod, p. 176, for example) and Kjesbu (2014) extends the liver index data presented by Hjort (1914) both backward and forward in time and use it to develop a unique 150-year-long condition factor time-series for Northeast Arctic cod. Ottersen *et al.* (2014) review the effects of biotic and abiotic drivers on the early life stage dynamics (from eggs to age 3 juveniles) of Barents Sea cod in the context of the hypotheses developed by Hjort (1914). They conclude that is unlikely that recruitment is, in general, always determined at the same single life stage. In fact, when summarizing the possible drivers of recruitment variability, Hjort said, "I had myself to leave these possibilities and their respective influence, if any, on the formation of the stock undecided, and the final decision in this matter may still be said to be open for discussion." (Hjort, 1926, p. 33).

Bergstad *et al.* (2014) report that strong recruitment years in a deepwater species, the roundnose grenadier (*Coryphaenoides rupestris*), are rare and that this must be carefully considered when exploiting long-lived fish with slow growth, high age at first maturity, and low fecundity (deep sea fish with life histories of this nature were not the focus of Hjort's work).

Several articles take up settlement by juveniles, another topic raised by Hjort (Hjort, 1914, p. 100, "Distribution of the youngest bottom stages"), although he did not address issues such as habitat structure/availability or density dependence. Bastrikin *et al.* (2014) report that the settlement dynamics of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) differs in timing, duration and in the size of individuals at the time of the pelagic-demersal transition. Caddy (2014) takes on the issue of habitat structure and availability, and its relationship with predation pressure and carrying capacity for demersal fish, using a novel fractal-based approach to quantify habitat complexity. Archambault *et al.* (2014) take up density-dependent processes during recruitment of 39 flatfish stocks. In general, settlement dynamics, carrying capacity of the bottom and concomitant density-dependence, has received less attention than they merit.

Hilborn *et al.* (2014) revisit the question of whether fish stocks that have been reduced to $<20\%$ of their maximum size exhibit signs of depensation (aka Allee effects). There was little evidence to support strong depensation, although they could not rule out the possibility of depensation at very low stock sizes. They also suggest that severely depleted stocks should rebuild is fishing pressure are reduced, but only if the environment has not changed. Hutchings (2014) also takes up the population dynamics of marine fish at low abundance, concluding that some severely depleted fish populations show signs of an Allee effect, or a transition from strong to weak compensatory dynamics. Like Hilborn *et al.* (2014), Hutchings (2014) notes that a population's sensitivity to environmental change increases the longer it remains at low abundance. Botsford *et al.* (2014) describe "cohort resonance" as a "characteristic behavior of age structured populations which does involve changes in adult abundance but can have a substantial effect on fluctuations in fished populations". It remains to be seen whether this fascinating phenomenon will be found in a wide range of stocks. Hixon *et al.* (2014) emphasize the importance of big old fat fecund female fish (BOFFFFs)—something that Hjort (1914) only alluded to peripherally when taking up maternal effects. The reproductive characteristics of BOFFFFs and the progeny that they produce indicate that they improve individual reproductive success in variable environments; this argues strongly for efforts to conserve them in the population.

It is fair to say that, for at least the past decade, global climate change has been a stronger motivator-focus of research in fisheries and marine science than has variability in recruitment *per se* (see Rice and Browman, 2014). Able *et al.* (2014) analyse a time-series of data on recruitment in the southernmost stock of winter flounder (*Pseudopleuronectes americanus*) and conclude that years in which spring temperatures were warm always experienced poor recruitment. They also took up the possible co-variability of temperature and predator abundance and the effect that this might have on mortality in winter flounder larvae. Zwolinski and Demer (2014) report that, during the last three decades, the periods of stock increase and decrease recruitment in the California Current Pacific sardine (*Sardinops sagax*) stock followed consecutive years with positive and negative Pacific Decadal Oscillation index values, respectively. Punt *et al.* (2014) assess whether incorporating environmental variability into management strategy evaluations improves the performance of those strategies. They conclude that including environmental factors only improves the ability to achieve management goals if their mechanism of action is understood. Importantly, although the context into which these studies are placed is climate change, the processes and mechanisms that they take up are the same as would have been the case if the context had been recruitment variability. Hjort (1914, 1926) also took up climate-related drivers of recruitment variability, for example, annual differences in freshwater run-off, sea surface temperature, and oceanic currents, and he was also well aware of climate-related changes in the distribution and range of stocks (e.g. Hjort, 1948, p. 164).

Since the themes taken up by Hjort (1914) deal with the factors that underlie variability in the productivity of ecosystems, and how that influences the population dynamics of high-fecundity organisms with low cumulative survival to reproductive age, I tried to attract contributions from outside the marine fish community. My success in that was limited, although there are articles herein on the drivers of population fluctuations in insects (locust) and invertebrates (octopus) (Cheke *et al.*, 2014; Sonderblohm *et al.*, 2014), which are entirely consistent with analogous studies on fish. Janssen (2014) and Pritt *et al.* (2014) assess whether the main mechanisms that influence recruitment variability in the sea apply in large lakes—the instances where they do, and where they do not, are instructive (also see Houde, 1994). Persson *et al.* (2014) also use freshwater vs. marine case studies to conclude that an ecological perspective that includes size- and food-dependent processes and, therefore, mechanistic linkages between trophic levels at multiple scales are needed to support a truly ecosystem-based management of fisheries. Bakun (2014) provides insights into the mechanisms of recruitment variability in the anchovies (genus *Engraulis*) and sardines (genera *Sardinpos* and *Sardina*) that exhibit different life history strategies in the face of changing conditions (on both short and long time-scales) (also see Zwolinski and Demer, 2014). All of these articles apply the compare-and-contrast approach, which can be a powerful lens to focus our thinking. Furthermore, broadening our perspective beyond fish and beyond the sea, and applying a compare-and-contrast approach to other systems, is a direction in which we should surely go, so these articles could also have been placed in the next section.

Where we are going

The remaining articles in this special issue give us a sense of where we might be going, and how we might get there. Rice and Browman (2014) track how "recruitment" research has developed since the 1920s and conclude that, in recent years, it has been subsumed into research on ecosystem-based management and climate change. They caution that this comes at a cost that should be recognized, and carefully considered.

Dickey-Collas *et al.* (2014) take up the challenge of categorizing approaches to modelling in fisheries science, recommending that trade-offs and limitations in modelling must be carefully considered in assessing their utility for decision-making in management. Subbey *et al.* (2014) present a review of stock recruitment forecasting focusing on challenges to predicting recruitment. They highlight the apparent failure of models to forecast recruitment even when environmental covariates are included, but offer insights into a way forward in their concluding remarks. Gaichas *et al.* (2014) apply a risk assessment approach to evaluate climate vulnerability for demersal and pelagic fish and benthic invertebrates in the Gulf of Maine and Mid-Atlantic bight. They use these case studies to demonstrate how a risk assessment approach can guide prioritization of short-term regional climate risk management action. Risk/uncertainty assessments are tools that are now being more widely applied in fisheries science.

Hare (2014) presents an overview of different approaches to thinking about and studying recruitment variability, concluding that we should focus on Hjort's approach: multi-hypothesis, integrative, and interdisciplinary. As Hjort said, ". . . it seems to me for several reasons desirable not to attack this important problem from any preconceived standpoint. On the contrary, the simultaneous investigation of meteorology, hydrography and biology seems the only way to a deeper understanding of the conditions in which the destiny of the spawned ova is being decided." (Hjort, 1926, p. 35).

In fisheries oceanography, traditional approaches to biological, physical, and chemical sampling occurs at spatio-temporal scales that typically far exceed those on which productivity-determining processes occur (e.g. predator–prey interactions; feeding). Godø *et al.* (2014) describe developments in acoustic technology that have the potential to provide quantitative knowledge and understanding of species distribution, abundance, and productivity-determining processes at the spatio-temporal scales on which they occur. If these technologies realize this potential we will be able to go far beyond where we have been and where we are now in terms of our descriptions and understanding of the processes that drive recruitment variability.

It has been a great privilege and honour to have motivated and overseen this special issue commemorating Hjort's most influential work. I can think of no better way to close than with his own words:

> It will be evident from the foregoing, that a study of the conditions which determine the numerical value of the year classes can only attain its object when based upon a very extensive plan. As a matter of fact, the object can *never be fully attained;* new questions will constantly arise, as *the knowledge obtained creates the demand for new,* and it will always be possible to increase and intensify our comprehension of the vital conditions affecting the organisms in question. A study of the fluctuations in the population of the sea, both fish and smaller organisms, and thus of the whole organic life existent in the ocean, is therefore the soundest possible basis for marine research, whether with theoretical or practical ends in view. There is moreover, scarcely any other question which is so well calculated to focus the attention of men engaged upon different branches of science. . . (Hjort, 1914, p. 209).

Acknowledgements

On 30 March, 2012, Christopher Taggart sent me an e-mail asking whether the Norwegian Institute of Marine Research—my employer and the institute at which Johan Hjort worked—would be doing anything to commemorate the 100th anniversary of Hjort's 1914 treatise. His e-mail served as the impetus for this special issue. I am grateful to Ian Sherman and Oxford University Press for generously making this special issue freely available. HB's editing work for the *ICES Journal of Marine Science* is supported by Project # 83741, "Scientific publishing and editing", from the Norwegian Institute of Marine Research.

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ICES Journal of
Marine Science

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ICES Journal of Marine Science (2014), 71(8), 1993–1999. doi:10.1093/icesjms/fsu108

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Where we have been

Original Article

A sea change: Johan Hjort and the natural fluctuations in the fish stocks

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Schwach, V. A sea change: Johan Hjort and the natural fluctuations in the fish stocks. – ICES Journal of Marine Science, 71: 1993–1999.

Received 19 January 2014; revised 12 May 2014; accepted 23 May 2014; advance access publication 25 June 2014.

That recruitment of juveniles to the stocks of fish is subject to natural variations is considered a scientific truth, if not a truism, in marine science. However, in 1914, when the zoologist Johan Hjort (1869–1948) published the notion, it meant a basic change in the understanding of the biology of the sea fish. A century later, his insight is a topic still at the centre of interest in fish biology. Hjort based his concept largely on investigations of herring (*Clupea harengus*) and cod (*Gadus morhua*) in the North Atlantic. He was the mastermind, but worked with a small group at the Directorate of Fisheries in Bergen, Norway, and in cooperation with the International Council for the Exploration of the Sea (ICES). The theory of natural fluctuations prompted an important step from migration thinking to population thinking, and gave the emerging fish biology and multidisciplinary marine science a theoretical basis. The article aims to explore the set of important facts and reasoned ideas intended to explain the causes for variations in year classes, and in this the fluctuations in the recruitment to the stocks. It argues that in addition to scientific factors, economic and political circumstances had an important say in the shaping of the understanding of stock fluctuations. The mere existence of a theory does not alone account for a breakthrough, and the article draws attention to the acceptance of scientific results.

Keywords: 1914, Bergen, fish biology, fluctuations, history of marine science, Johan Hjort, Norway.

Introduction

The understanding that the recruitment of juveniles to the stocks of fish is subject to natural variations was published in an ICES publication entitled "Fluctuations in the great fisheries of northern Europe" (Hjort, 1914; hereafter 1914-theory). The explanation was mainly based on investigations on herring and gadoids, especially cod in northern Atlantic waters, stocks to become model species for fish biology and management. The theory of the varied strength of the year classes as a cause for natural fluctuations in the stocks was significant as it laid the base for the present understanding—and in 2014, a century of research to deepen the knowledge of the various, and active biological and physical factors. The notion provided the newly founded community of ICES with a much looked-for theoretical foundation in the investigations of the fish. Fish biology was in formative years a core field in multidisciplinary marine science; hence, tracing the realization of the 1914-theory also means to contribute to the understanding of the shaping of marine science before World War II. The concept of natural fluctuations and its background is examined through a biographical lens as the profile of Johan Hjort—the main intellectual force behind the theory—is drawn.

The zoologist

Hjort's social background was the, in percentage, small, but influential, administrative, and political elite of civil servants (embetsstanden; Myhre, 2008). His father, Johan S. A. Hjort, was a professor of ophthalmology at the National/University hospital (Rikshospitalet), while his mother came from the Falsen-family, which like the Hjort's descended from Denmark, and had moved to Norway to take up positions as civil servants, merchants, and craftsmen. Johan grew up as the oldest of six siblings in the small, but rapid expanding capital of Kristiania (renamed Oslo in 1925). He was intended for a career in medicine, like his father and grandfather on the paternal side, but was, after 2 years of study, allowed to change to zoology. Until 1905, no complete academic degree in zoology existed in Norway. Germany was an

Figure 1. Johan Hjort was a well-regarded marine scientist, but also a controversial Director of Fisheries, known for his somewhat volcanic temper. "His personality was so powerful and his views so decided that he was apt to impose them on others, and he was not very receptive of views that differed from his own. But he was a great figure whom his colleagues and friends regarded with respect, admiration and affection, even when they differed from him "(Russell, 1948). Illustration: Courtesy of the family Hjort by Harald Hjort.

obvious choice, and a request was sent to the well-known professor in zoology, Otto Hertwig at Ludwig-Maximillian-University in Munich (Schwach, 2000: 64–65). The civil servants were influential, but on average not a wealthy social group; only with careful financial planning, and a scholarship from the University, was Hjort's education realized (Hjort, 1891–1904, 1891–1893; Hjort, 1893b). During the years abroad, the father wrote regularly, providing the son with familiar and local news—and a century later, historians with a valuable source to understand Hjort's pathway to fish biology (Hjort to Hjort, 1891–1904; Figure 1).

In the 1880–1890s, important changes in life sciences took place, and the marine environment stood in the forefront. The first marine zoological/(biological) stations had emerged at Nice, Naples, and elsewhere, and they became key loci for developmental morphology and other evolutionary studies. Hjort's education followed a mainstream programme, in years when the previous preoccupation with taxonomy, systematics, and morphology shifted towards evolutionary questions. He attended basic courses in the Bavarian inland, and had to study marine specimens preserved in spirit. In 1891, Hjort had a desire to spend summer vacation at the marine biological station in Villefranche-sur-Mer, Nice. The family's economy did not allow such an expense, and the son was called upon. Instead of southern France, he spent the University vacation in Norway, and sailed to Bergen for a visit to Bergens Museum. Here, Hjort discovered the abundance of marine life at the western coast of Norway, and the joy of access to fresh material (Schwach, 2000: 65–66). When the winter term started, the student travelled back to Munich, and began, early in 1892 to work on the graduation thesis. It dealt typically with marine invertebrates and the question of the early stages of development of the ascidians (sea squirts): the formation of germ layers and specialization into specific tissues and organs in the family of Botryllidae, and especially the development of the nerve system. A sojourn at the station in Naples in spring 1892 complemented the research. Here Hjort worked with fresh material, and felt unlike in Munich, the pleasure of scientific discussion on an equal footing.

The young man and the sea

In January 1893, Hjort obtained the doctoral degree in zoology (Hjort, 1893a, b).

When the 24-year-old zoologist a month later arrived in Kristiania, he was awaited not only by his family, but also at Norway's only University, "Det Kongelige Frederiks Universitet". The zoologist and explorer Fridtjof Nansen (1861–1930) was eager to be relieved from his duty as curator at the Zootomic Museum (a forerunner of the zoological laboratory), to set sail with *Fram* and leave for polar areas. Hjort stepped in for Nansen. As an adjunct position, he was appointed research fellow for the sea fisheries (fiskeristipendiat) by the Ministry of the Interior, as the hitherto fellow Georg Ossian Sars (1837–1927) no longer wanted to carry the burden of outdoor work on the fishing grounds. Sars had been involved almost since 1860, when Norway as the first country established a commission for scientific fisheries investigations (Schwach, 2000: 19–52). To find a successor had not been an easy task. In 1890, the British professor W. C. McIntosh noted that the Norwegians were interested in developing a centralized fisheries board, but had not yet identified the suitable man to direct it (Macintosh, 1890). Hjort took, against the advice of his father, the position (Hjort, 1891–1904: 3 April 1892). Sars got assistance, and 3 years later, in 1896, he passed the responsibility completely on to Hjort. The payment as fisheries fellow was nearly twice the wage of the curator position (Schwach, 2000: 69), not a triviality for a man who was about to marry and maintain a family (Figureido, 2002: 19–28). But even more than the salary, Hjort probably was excited by the chance to work in the field—at the ocean. In general, the association between sport, field studies, and science was strong among naturalists, and it took a special form in Scandinavia due to climatic conditions and partly influenced by the polar researcher's expeditions and adventures (Schwach, 2000: 69–70). Natural sciences in Norway were dominated by disciplinary cultures founded upon fieldwork before 1940. For Hjort, the field meant the North Atlantic, and "the hazardous work of carrying on continuous scientific investigations in the storm-swept waters of the North Sea", as the American zoologist, Charles A. Kofoid in 1908 summarized his impressions of the ongoing research in Bergen (Kofoid, 1910: 298). Enthusiasm for outdoor scientific work, intertwined with solving practical problems of the fisheries, led marine researchers like Hjort to the sea. Still, 1895–1896, Hjort went back to Germany for studies in physiological chemistry and further cell studies, but by 1900, he turned his attention to what became a lifelong commitment to commercially important fish and marine species. But, exactly what motivated a young marine zoologist, with promising prospects of a university career, to choose fish biology, a discipline in its very first beginning, is not known.

With a face turned to the ocean

The Norway Hjort returned to was, with its 2 million inhabitants, a sparsely populated country, where the majority lived closed by the shores of thousands of miles of seacoast. The sea and its fish were of vital importance for the national economy, as especially from 1815 to 1880, a substantial income was gained from extensive maritime trade and export of fish, making surplus capital available, which again contributed, to reinvestments and domestic growth. Despite the fishing industry's declining relative significance from the 1880s, it remained vital both to the economy and to the population along the long coast. The political recognition of the sea fisheries went hand in hand with the government's willingness to modernize, that is, adapt the industry to a capitalistic economy. The political attention to the fishing industry included also laws and regulation, public supervision, and economic statistics. Owing to the importance of the large seasonal catches of cod and herring for export income, the Norwegian government's interest had from 1860 a main point in the migrations of cod and herring; in this respect, the investigations were very specific. Scientific investigations were considered an appropriate way to establish basic knowledge of the ocean and its resources. In addition, the scientists served as strategists for modernization in a primary industry and occasionally as its implementers. Hjort became the foremost entrepreneur in the history of the Norwegian marine science with his aim to integrate a scientific with an economic perspective to establish a scientific discipline, as well as a scientific-based fisheries management and a capitalistic fishing industry (Schwach, 2000: 128–132; Schwach, 2013). In a national (and Nordic) context, marine science is one example of a trust in a science-based, instrumental rationality to solve pressing political and economic issues (Sörlin and Warde, 2007: 124; Asdal, 2011).

A national, Scandinavian, and international momentum

The Swedish chemist-turned-oceanographer, Otto Pettersson (1848–1941), wrote a letter to the newly appointed fellow (Hjort to Pettersson, 1893–1901, answer of 3 January 1893). In this, he suggested incorporating surveys on physical and biological properties of the sea, and coordinating the Scandinavian efforts by regular and agreed short surveys four times a year. Hjort agreed and joined Pettersson's programme (Hjort to Pettersson, 1893–1900; Pettersson to Hjort, 1893–1900; Schwach, 2000: 70–71). Both Pettersson and Hjort was among the Scandinavian scientists who committed themselves to founding ICES in 1902, and Hjort's career became linked to the Council in terms of establishing its scientific foundation and building it as an organization.

In the last decades of the 19th century, a desire to understand the underlying causes of fish distributions and the total amount of fish in the sea led managers and scientists, whose concerns reflected the economic importance of the fisheries in their countries, to seek for ways to organize the public efforts. These efforts would include both artificial hatching and studies of biological and/or physical conditions of the seas around the states (Rozwadowski, 2002: 9–41). ICES combined marine science with the needs for (a scientific based) management of the fisheries, and was from 1900 to 1940, the principal community for studies of fish, biological, and physical properties of the ocean (Mills, 1989: 75–186; Rozwadowski, 2002: 3). The early programme of ICES' was an outcome of the previous Scandinavian surveys, mixed with a widespread concern that humans drew too heavily on the fish stocks, and thus an urge to investigate the assumed overfishing in the North Sea and in the Baltic Sea. The Scandinavians, in particular the Norwegians, did hardly see variations in the catches in terms of overexploitation. In fact, the fishing resources, especially herring, were, until 1969, thought of as a horn of plenty and were, if regulated, only temporarily. Hjort in 1899 stated his motto "fish more", an axiom he kept all his life (Dahl and Hjort, 1899: 133–136; Schwach and Hubbard, 2009: 38–40).

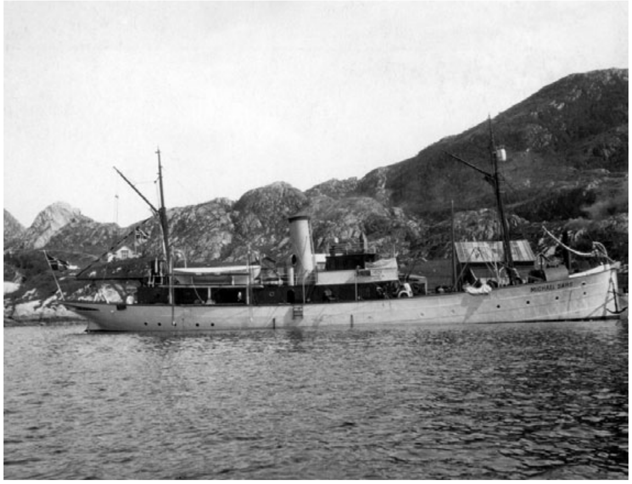

Figure 2. *Michael Sars* was an English trawler rebuilt at Fredrikstad Mekaniske verkstad, Norway. She was 125 ft long, with a beam of 23 ft, draught 12 ft, tonnage 226 grt. *Michael Sars* had a coal-fired steam engine, 300 hp, but was also rigged for sail. Illustration: Courtesy of Institute of Marine Research.

Heading back to Norway

In October 1900, Hjort sailed to Bergen with *Michael Sars*, the newly purchased vessel of the Board of the Fisheries (Fiskeristyrelsen) and Hjort's most important tool for investigations (Figure 2). He was to take up a position as leader for the scientific department in the triumvirate of the Board. After a reorganization in 1906, Hjort became the sole Director at the Directorate of Fisheries (Fiskeridirektoratet; Schwach, 2000: 89–92, 98). The establishment of a new national management was aimed to unify a range of—partly crossing conflicting—interests within the sea fisheries. A governmental agency with management and science integrated under one roof was internationally seen a unique way to run fisheries issue in 1900, but turned out to be profitable for marine science. ICES and governmental agencies such as laboratories and fisheries boards with full-time positions for scientists, regular financing, offices, and research facilities like access to vessels for surveys did more to shape marine science than singular expeditions and biological stations.

Bergen was closer to the important fishing districts than the capital, and in this regard, a natural choice. However, Hjort imposed a condition for taking up a position in Bergen: the Board should be a sole organization, independent of Bergens Museum (Schwach, 2000: 86). This clause however did not hinder him seeking cooperation when Hjort himself or the fisheries investigations could benefit therefrom. The sojourn in Naples probably inspired the way Hjort organized his investigations in Bergen: it was a group of handpicked peers and assistants—a talented group, but one of inherent instability. With a vengeance, Hjort combined national and international investigations (Schwach, 2002). In ICES, the Bergen-group communicated their ongoing research and learned about work elsewhere. The formal and informal network undoubtedly strengthened the group in Bergen, as contact and collaboration was vital to maintain a high scientific standard in applied research, investigations undertaken close to the immediate needs of the fisheries management. In the Parliament, the obligations towards ICES were considered a national duty, and served to protect domestic investigations against attempts to cut down financial support, especially for the costly maintenance of *Michael Sars*. Besides, the maritime sphere, including shipping, polar research and marine investigations were a source of national pride, fields where Norway could and should shine.

Migrations gave way to natural fluctuations and populations

From the 1880s to 1930, a gradual shift from "migration thinking" to "population thinking" took place in the discipline emerged as fish biology (Sinclair and Smith, 2002: 297–304; Smith, 1994). The notion of migration was developed for herring and by analogy applied to cod (Hjort, 1914: 2–5). Hjort with his 1914-theory played an important part in the shift. The novelty of Hjort's scientific programme lay in its field studies—a broad approach to solve the enigma of the large variations in the fishing catches: the combination of physical oceanography, biological oceanography, and fish biology. In fish biology, surveys of all stages of fish: eggs and larvae, pelagic and demersal juveniles and adults were of importance (Sætersdal, 2009: 19). Focus in this section are single factors that had a particular play in providing a fertile ground for the shaping of the 1914-theory, and will include the issues of hatching cod, a method to distinguish the schools of herring, and demographical statistics.

Hatching, a local issue with overarching scientific consequences

Hatching was 1880–1914, especially in the Anglo-Saxon countries, a widespread way to improve and secure a stable recruitment of fishing resources (Cadigan, 2009: 76–80; Schwach, 1999: 27–28). In Norway, the Flødevigen hatchery (Flødevigen Udklækningsanstalt) was built in 1884 nearby the town of Arendal, and formally a branch of the semi-private Society for Development of the Norwegian Fishing Industry (Selskabet for De Norske Fiskeriers Fremme). The hatchery was for a large part financed by local funding. During the days of sailing, Arendal was a prosperous town owing its wealth to the shipbuilding yards, and local surplus capital was available. Gunder M. Dannevig (1841–1911) was a driving force; the methods and technical solutions at Flødevigen including the hatching tanks seem to have been the foremost of their kind (Kofoid, 1910: 296–297). Alas, Arendal's wealth ended abruptly in 1886 due to a profound technological change: steam surpassed sail. Private revenues disappeared, and Flødevigen became depended upon public funding. The Parliament decided to evaluate the economic benefits of hatching. Reliable fish statistics was non-existent; so the parliament suggested to mark the larvae, and set aside funding for a marking experiment. The task was handed over to Hjort who asserted that it was impossible to mark newly hatched larvae; thus, an eventual gain of artificial hatching vs. natural production could not be measured (Stortingsforhandlinger, 1895). Hjort wrote to one of the very few experts in fish biology at the time, the Dane C. G. Joh. Petersen (1860–1928), asking him for advice in this debated issue. Petersen answered by stating his skeptics to the usefulness of hatching (Petersen to Hjort, 1896–1927, 26 February 1895). A fortunate sequel of the question was that Petersen became Hjort's first teacher in fish biology, soon turned to sparring partner (Petersen to Hjort, 1896–1927).

In 1899, Hjort pointed out that it was not possible to keep the larvae alive after the first stage when they fed on the content of the yolk sac. The death rate became extremely high at hatching stations in both the United States and Norway (Dahl and Hjort, 1899: 141). The statement was underpinned by referring to Sars' observations on the high death rate among yolk sac cod larvae (Sars, 1879: 27). Dannevig did not give up his mission. In 1900–1902, he represented the county in the Fisheries Council (Fiskerirådet)—an advisory council to the Board of Fisheries. At the meeting, he proposed to count the numbers of larvae (0-group) in fiords where larvae were hatched and released, and compare the numbers with fiords with no release of cod larvae. Hjort's assistant, Knut Dahl (1871–1951) an outspoken opponent of hatching was put on the task and counted the number of larvae in 1903, 1904, and 1905 (Schwach, 1999: 40–41). Not surprisingly, Dannevig and Dahl's findings were diametrically opposed; but important for Hjort was Dahl's observation that in years rich in fry, the large numbers were common to a long stretch of the coast, while in years with few fry; the poverty of numbers was demonstrated in all fiords (Dannevig, and Dahl, 1906). According to the concept of migration, all the cod in Danish and Norwegian waters belonged to *one* sea stock migrating over large areas (Dahl and Hjort, 1899: 53–54). Around 1904–1906, Hjort may have started drifting away from the view that migrations were *the* essential point to comprehend the variations in recruitment from year to year. The difference between small and large annual classes of larvae could it affect the catchable stock?

Herring with a certificate of birth and population

At the inaugural ICES-meeting, three committees were set up. Hjort was elected "convener" of the Committee A—"the migration-committee" (Schwach, 2000: 148–149). The large fisheries after cod were a typical feature for Norway, whereas the herring was a natural resource important in the majority of the member-countries. In 1905, Hjort decided to continue studies on cod, but also intensify the herring investigations at home and in the "migration-committee". He saw it as an opportunity to concentrate the work on joint species, strengthen the ICES-community, and convince, in the many countries hesitant managers, about the practical value of the fisheries investigations. The omnipresent Pettersson agreed (Pettersson to Hjort, 1894–1939, 15 February 1905; Schwach, 2000: 155). This way cod and European plaice (*Pleuronectes platessa*) but foremost herring in an early phase became model species for fish biology (Stephenson and Clark, 2002).

Friedrich Heincke (1852–1929) at the German scientific commission (Die Deutsche wissenschaftliche Kommission für Meeresforschung) and member of the "migration-committee", had after 20 years of measuring meticulously herrings from different waters, reached the conclusion that herring comprise geographically distinct spawning stocks (Heincke, 1898). First, using Heincke's method, Hjort and assistants classified the spawning populations in "Norwegian waters" (Hjort to Heincke, 1902–1911; Schwach, 2000: 141–144). The age of the herring was decided customary by measuring its length (Hjort, 1914: 16–18). Heincke's procedure to distinguish the herring stocks was very time-consuming, a serious disadvantage in Bergen where the men were few and the ocean large. The herring in barrels waiting to be measured decomposed, and due to the smell and complaints from the neighbours, the scientists were forced to remove the barrels (Koefoed and Broch, 1962: 28; Schwach, 2000: 148–152). One can easily assume that Hjort was stressed by the situation. In 1904, Hjort remembered a technique of age determination in fish by scales and otoliths, brought to his knowledge by German peers 4 years earlier, but of which he then had not taken notice (Hensen to Hjort, 1900, 5 December 1900; Heincke to Hjort, 1902–1907, 12 December 1903). Could the scales or otoliths of herring give any useful information about size/age, growth, and spawning? He found it worth trying, and let a young assistant, Hjalmar Broch (1882–1969); Broch, (1906) and later Dahl (1907) tests this method. Broch showed that the scale was an adequate means to a precise determination of the age and of growth patterns of the herring. He also proved systematic differences in the growth rate between different spawning populations. Einar Lea (1887–1969) refined the methods and technique (Schwach, 2000: 152–159, 166–167). Heincke's method was set aside; from 1907, the herring's growth zones, in particular the winter rings were used to determine the age, growth, and which spawning stock the single fish belonged to (Hjort, 1914: 18–21). The investigation in 1908 revealed that the herring did not reproduce evenly, rather large variations from one year to another was the norm. Herring from 1904 was overrepresented of all the herring caught and counted. The next year, in 1909, this year class added up to 77% of the total. The nature yielded a large year class in 1904—a generous gift to the fish biologists (Schwach, 2000: 159–160).

Widows, orphans, and the population of herring

An incidental linking between natural science and an expressed need for a social reform became another turning point for the fish biologists in Bergen. Hjort was first introduced to (descriptive) statistics through Heincke's work, and in practice by a report to the Parliament on mandatory insurance for fishers (Schwach, 2000: 157–158). In their application of statistics and biometrical methods, the Bergen-group was in vogue in zoology. The local backdrop was a terrible disaster at sea offshore of Titran, a fishing village on Frøya, in the county of Nord-Trøndelag. On a stormy night in 1899, 120 fishers lost their lives, leaving behind widows and children in poverty. In autumn 1906, Hjort, in the capacity as Director, was requested to head a public committee, and write a proposal on accident and death insurance for fishers (Stortingsforhandlinger, 1907–1908; Norsk Fiskeritidende, 1907: 135). Parallel initiative was taken for other groups of workers, in years before pensions, death and compensation insurances were coordinated and made general (i.e. The National Insurance Scheme, 1967; Seip, 1984: 174–175). In writing the proposal, Hjort cooperated with the renowned actuary Andor Hoel, from 1908 the first director of the public service pensions fund in the municipality of Bergen (Bergens kommunale pensjonskasse; Sollied, 1932). During the work, Hjort was exposed to demographic statistics, a field in which domestic statisticians had gained a good knowledge (Lie and Roll-Hansen, 2001). To stipulate the cost of the insurance premiums to be paid by the single fishers to compensate—economically—for the loss of income, the actuary calculated the numbers and structure of the population of the fishers and their families. The estimations included the age composition of all men recorded in the national census as fishers, estimations of birth and death, and the average number of children in the group. Hjort noticed that the year classes in the fishing population were not of equal size, and the population pyramid changed over time. It struck him that the methodology of demography might be useful to understand the patterns of the fish stocks: "As I [Hjort] was occupied with the question about an accidental insurance for the fishermen, it occurred to me that one could gain deeper substantial and deeper understanding also of the fish stocks by examining the age compositions in the various herring stocks " (Hjort, 1911). Consequently, Hjort transferred his newly gained knowledge to the population of fish. At this point, the position as Director of Fisheries, with the responsibility for the national statistics of the fisheries, and employees with experience in collecting statistics, certainly was no disadvantage (Nordstrand, 2000). For the fisheries, Hjort assumed a linkage between the amount of fishers' catches and the sizes of the year classes, in that a rich annual class will affect the adult, catchable stock.

The last, critical stage

Hjort's work was met with critics in ICES. British (marine) zoologists, in ICES foremost represented by Wentworth D' Arcy Thompson (1860–1948), had taken an interest in biometrics. Hjort and Thompson over herring scales collided in 1910 (RP, XI, part B, app. D, 1909: 64–66). The dispute ended only in 1938 (Schwach, 2000: 171–176). Hjort asserted that the rings on herring scale reflected precisely the age/years of the herring, the counting winter rings being a core in research programme in Bergen. Thompson claimed that the age-determination of herring was inexact (RP, XIX, part B, app. D, 1913: 102–104). He also believed that scale rings were a physical—optical—phenomenon only. In retrospect, the advantage of the controversy was the demand felt in Bergen to elucidate the method for counting the winter rings of ageing on the scale and its technique. Another point of critics seems to have been that Hjort ran the committee A as a branch of the Norwegian investigations, and that the publications of the committee's report exceeded the budget (Schwach, 2000: 165). In 1909, ICES' structure was changed, and the three initial committees were discontinued (Rozwadowski, 2002: 52–53). Hjort was offered a small sum to continue the investigations on herring-scales. The scientific results to be presented as the "Fluctuations in the Great Fisheries of Northern Europe" were, in its concluding phase, much of a national project (Schwach, 2000: 164–170). By 1909, Hjort probably had a hunch that he was on a track worth following: the cause of the fluctuations in the spring herring fishery was the success or failure of the year classes composing the stocks. Additional surveys supported his view: Bjørn Helland-Hansen (1877–1957) investigated haddock (*Melanogrammus aeglefinus*) in the North Sea (Helland-Hansen, 1909), Désiré Damas (1877–1957) examined cod and other gadoids' eggs in the northern Atlantic 1900–1906 (Damas, 1909), and Dahl reported yearly variations in the North Sea (Dahl, 1909; Sinclair and Smith, 2002: 300–302). Hjort likely became certain of variations in the annual classes of herring and gadoids, and sometimes between 1910 and 1913, he first formulated the hypothesis that the larval stage was of paramount importance for the size of a year's class. He discussed whether either predators ate the eggs and/or the possibility that physical conditions such as the temperature of the water or its salt content were decisive for the size of a year's class. Hjort believed that to survive a critical stage, it was essential that the larvae had sufficient food (Hjort, 1914: 202–207).

Presentation, war, and acceptance

The 1914-theory in its entirety was presented in an evening lecture on 16 September 1913 in Copenhagen, during the annual ICES-meeting (RP, 1913. XIX, part B; app. D, 102; RP, 1915. XXI, part B, 16–20). In spring 1914, the publication was printed: volume XX of the ICES', "Rapports et Procès-Verbaux" (Hjort, 1914). At the same 1913-meeting, a herring committee was set up

Figure 3. Johan Hjort, photo presumably taken during the Canadian fisheries expedition, 1914/1915. "Hjort was always happy in a ship", stated his long time British colleague H. G. Maurice in an obituary (Maurice, 1948). Illustration: private, Vera Schwach (photographer not known).

(RP, 1913. XIX, part B, annex A, 60). By May 1914, and after an excursion to the spring herring districts on the west coast of Norway to investigate and agree upon the methods and standards for sampling, the committee drew up a plan for investigations in the ICES-member countries. The plan embraced both fish biology and "hydrographical observations", and it reflected the two overarching issues in fish biology: overexploitation and/or natural fluctuations of the natural resources of fish (RP, 1915. XXI, part B, 1915: 16–20).

Dark skies covered Europe, and in July, World War I broke out and interfered with ICES including the joint herring investigations. The warfare forced ICES to keep its activity at a minimum and hampered the distribution of the 1914-theory. By 1918, the situation had changed. In 1914, the military requisitioned *Michael Sars* to safeguard Norwegian neutrality. In 1917, owing to an argument with the Norwegian government about neutrality and fishing exports to the United Kingdom, Hjort resigned and left Bergen. Germany withdrew from the ICES in 1915 and only returned in 1926 (Went, 1972: 51, 68), giving the United Kingdom a larger influence in the ICES. Only in 1929 and 1930 was Bergen's method and results from 1914 accepted fully in the ICES (Sætersdal, 2009: 25–26).

Conclusion: fluctuations in fish biology

Johan Hjort was a highly qualified and promising marine zoologist who linked the new developmental marine zoology with the emerging fish biology. Hjort should be noted for his ability to transformed economic and political problems into research questions, his daring in formulating risky hypotheses, a groundbreaking theory, and the ability to convert scientific knowledge for the use of management of the sea and its marine resources. He was politically shaped by, and worked in a domestic and international situation that favoured scientists who offered both a basic and practical mode of pursuing scientific investigations. The work in Bergen is one early example of how governmental agency with full-time positions for scientists, regular financing, offices, and facilities such as vessels for surveys did shape modern marine science. Culturally seen, Hjort was part of a disciplinary culture dominated by work in the field. The willingness to work onboard the research vessel and make cruises in all seasons and weather conditions of the year was a premise for Bergen's broad approach to marine research (Figure 3). The 1914-theory was a possible, in no way predetermined outcome of investigations on fish and the ocean in Norway and Scandinavia since 1860, and in ICES after 1900.

The novelty of Hjort's scientific programme lay in its field studies—a broad scientific approach to solve the enigma of the large variations in the fishing catches, combined with specific economic and pressing research questions. While fisheries researchers tended to focus on the fishable stock, Hjort partly owing to his academic training, the work of the predecessor G.O. Sars, and a controversy over hatching, came to focus on the early stages of the life cycles of fish. In addition to hatching, a method to distinguish the schools of herring, and demographical statistics played a prominent role. From the understanding of the awareness of natural variations between different year classes and the larva stage as critical for the size of an individual year's class arose the notion of the natural fluctuations in fishing stocks and the question of the significance of the early "critical stage".

World War I discontinued the research, which had constituted Bergen as a centre of fish biology. The mastermind had disappeared, and in the remaining researchers, there were hardly anyone with the same intellectual capacity and political influence. The ocean-going vessel, the most important tool—essential to undertake surveys of the highly migratory fishing stocks of cod and herring in the North Atlantic—was gone. Differences in the economic and scientific interests of Norway and most of the ICES members may also explain the loss of Bergen's leading position. After 1918, the attention of fish biologists in "North Sea-countries", under the leadership of the UK, was directed towards investigations of the commercially important stocks of ground fish, and the presumably overexploitation of the stocks.

Acknowledgements

I thank the referee Mike Sinclair and the editor for their most useful comments and critical questions.

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ICES Journal of
Marine Science

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Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Johan Hjort: The Canadian Fisheries Expedition, International Scientific Networks, and the challenge of modernization

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Hubbard, J. Johan Hjort: The Canadian Fisheries Expedition, International Scientific Networks, and the challenge of modernization. – ICES Journal of Marine Science, 71: 2000–2007.

Received 4 February 2014; revised 17 April 2014; accepted 19 April 2014; advance access publication 12 June 2014.

By leading the Canadian Fisheries Expedition of 1914–1915 Johan Hjort took the opportunity to do far more than just survey herring, other fish stocks, and the hydrography of Canadian Atlantic waters. He also attempted to improve the backward fish-processing technologies used in the local fisheries, an agenda blocked by the Canadian government. Hjort did succeed markedly, however, in introducing Canadian scientists to the International Council for the Exploration of the Sea's new scientific methods for fisheries research. He and his colleagues offered training in the new dynamic oceanography as well as population demographic studies and biometrics for studying fish populations, races, and other units. His extroverted leadership-initiated lasting linkages between Canadian and Scandinavian scientists, and created an international network of fisheries biologists.

Keywords: history of Canadian science, history of fisheries biology, Johan Hjort.

Introduction

The 2008 celebration of the hundredth anniversary of Canada's St Andrews Biological Station (formerly the Atlantic Biological Station) was marked by presentations of histories of its many research programmes. A running theme in the papers was the role of Johan Hjort's Canadian Fisheries Expedition of 1914–1915 (Hubbard *et al.*, in press). Hjort amply merited this recognition, as his contributions were foundational to Canadian fisheries biology and oceanography as focused scientific disciplines. The Canadian government had funded Canada's first permanent marine research facility in St Andrews in 1908, but the university-based volunteer researchers conducting summer investigations were capable of only a parochial treatment of fisheries issues. Few had any Maritime background, and while several biologists enthusiastically researched fisheries problems, they lacked the experience to create coherent or long-range research programmes. When, in 1914, the Biological Board of Canada requested Hjort to lead the Canadian Fisheries Expedition, the stated intent was to have this Norwegian scientist locate and identify herring "races" and assess the potential for exploiting existing and as yet unidentified stocks. The scientists' deeper agenda was to have Hjort train Canadian expedition participants in advanced fisheries research methods that he and others were developing under the auspices the International Council for the Exploration of the Seas. Indeed, they hoped to hire the 46-year-old "greatest living authority on fish and the fish industry" permanently (Macallum, 1914). Although this was not to be, Hjort's leadership of the Canadian Fisheries Expedition was indeed seminal in establishing a solid fisheries research programme in Canada, one that flourished for decades thereafter under the auspices of the Biological Board of Canada (after 1937, the Fisheries Research Board of Canada). Beyond this, Hjort instilled a culture of modernization within Canadian fisheries science, and his dynamic leadership led Canadian scientists to establish and develop contacts in Scandinavia and the United States, beyond traditional British imperial links. Hjort drew Canadian scientists into the international research network that he and other ICES scientists were nurturing as they developed the nascent discipline of fisheries biology.

Hjort and the Backward Canadian Atlantic Fisheries

Hjort led the Canadian Fisheries Expedition on the heels of publishing his seminal *Fluctuations in the Great Fisheries of Northern Europe* in 1914. In part he was building on earlier oceanographic studies: in

1910 he and Sir John Murray had used the *S.S. Michael Sars*—the research vessel of the Board of Fisheries in Bergen, Norway—to survey Northwest Atlantic waters. But when Hjort, who served as Director of the Fisheries Directorate in Bergen, requested the Norwegian government for a leave of absence in 1914, his stated aim was verifying his year-class theory of stock fluctuations beyond Eastern Atlantic waters. Adverse research conditions in Norway following the outbreak of the First World War, and Canadian government funding for the project, contributed to the Norwegian government's willingness to grant him this leave.

Hjort arrived in October and carried out an energetic 2-month survey of fisheries and fish-processing practices. He travelled northward along the coast, starting from Boston, Massachusetts and visiting fishing ports in New Brunswick, Nova Scotia, the Magdalen Islands, and Newfoundland and Labrador. He collected scale samples to analyse the growth rings of samples from the fish catch, and thereby determine the age structure of the inshore fished populations; he observed working fisheries, examined local fishing gear, and talked to fishers and businessmen. Proceeding to Toronto, he remained until early January collating and analysing the samples and data thus obtained. His expenses for this preliminary work were covered by the Biological Board of Canada.

Hjort was not impressed by primarily coastal or inshore nature of the fisheries, carried out through gillnets. He advised Canadian scientists and bureaucrats that Canada should develop an offshore driftnet fishery for herring that would at the very least provide the Grand Banks schooner fleet with much-needed bait for the cod fishery (Hjort, 1914a). From his preliminary survey, he recommended a full oceanographic expedition for the following year, while conducting experimental fishing using nets capable of catching a full range of age classes of herring and other fish. He proposed to discover "whether the sea off the coasts of Canada and Newfoundland has these immense riches yet untouched by the Canadian fishermen", and thus if a new kind of herring fishery would be possible in Canadian waters (Hjort, 1914a).

Hjort did not comment on the parallels he must have seen between the Canadian and Norwegian fisheries. While he was particularly distressed by the backward fish-processing techniques and poor quality of Canadian fresh and frozen fish, he would have found the levels of fishing technology familiar. Neither Norway nor the Canadian Atlantic had any significant industrialized fisheries until after the Second World War (Schwach and Hubbard, 2009). The fishers of both nations relied mainly on sail and traditional fishing methods. Perhaps because of their similarities, he thought he had some insights into how to improve the profitability of Maritime fisheries. About a third of his proposal was focused on using the expedition to train fishers in the use of a new, and patented, Norwegian fast-freezing method—the Ottesen method. Newfoundland fishers, he noted, waited until the first frosts to freeze herring, limiting supplies of this product as bait. He considered improving fish preservation by freezing "of the greatest importance for the establishment of an enlarged herring fishery" (Hjort, 1914a). Hjort promoted this idea with fishing industry leaders, and this proposal was strongly endorsed by the Halifax, N. S. Board of Trade (1914). The Department of Marine and Fisheries would have none of this, however. Hjort was so upset by the rejection of what he saw as an essential component of the whole programme that he almost cancelled the expedition (Hjort, 1914b).

What Hjort failed to realize was that Norwegian and Canadian markets for fish were vastly different. In Norway the fisheries were an important component of the economy and the Norwegians relied heavily on seafood in their diet. In Canadian and US urban centres and inland markets, people had a low regard for sea protein, preferring the New World's affordable beef, pork, and chicken. The backwardness in fish handling that he witnessed was a product of this weak demand for fresh or processed fish, which meant that the major markets for Atlantic Canadian and Newfoundland dried and salted cod, and other pickled and smoked fish, were located in the West Indies and Brazil and South America, with some markets in Catholic European countries like Spain and Italy (Grant, 1934). There was a limited North American market for canned seafood, but these products were generally locally caught before canning and the Canadian product had problems that could not be addressed by fast-freezing methods. The Atlantic fisheries were not highly regarded as a source of wealth. Canadian fisheries officials were content to encourage the industry by training fishers to adopt the best practices of long-established methods; they believed that emergence from its primitive conditions would only come when the Maritime fishing industry adopted British industrial fishing technologies such as steam-powered vessels that would enable fishers to capture better quality offshore fish (Mills, 2009).

In the meantime, Department of Marine and Fisheries officers gave Maritime fishers demonstrations of superior versions of traditional methods, such as Scottish smoke cures for salmon and haddock, or Norwegian methods for pickled herring. Since 1904 it had hired several experienced Scottish fisheries overseers to establish a voluntary programme to help Maritime fishers learn to make tightly coopered fish barrels and to train them in improved smoking, pickling, salt-cure and dry-cure methods (Hubbard, 2006). This programme made little headway.

Unlike the conservative Canadian bureaucracy, Hjort was an ardent modernizer who demanded that fisheries science provide practical outcomes for the fishing industry. In Norway, he promoted new fishing methods and expanded the number of species exploited by Norwegian fishers, himself pioneering Norway's first shrimp fishery and developing a new net design to facilitate this (Søndergaard and Schwach, 2009). While Canada's Commissioner of Fisheries, Edward Ernest Prince (1858–1936), who was Chair of the Biological Board of Canada, and Archibald Byron Macallum (1858–1934), its Secretary Treasurer, both endorsed promoting the Ottesen fast-freezing method to fishers, the Department of Marine and Fisheries saw no value in this work, and flatly rejected it. Hjort continued to plead for his scheme, telling Prince: "I am convinced that an effort to solve the great actual practical questions must embrace their most important sides" (Hjort, 1914b). He contended that he could not carry out an expedition if it did not "correspond [...] to the lines expected by the supporters: the Board of Trade of Halifax. I do therefore prefer the scheme to be withdrawn to endangering the possibilities of the success of the expedition" (Hjort, 1914b). J.G. Desbarats, the Deputy Minister of Fisheries, turned a deaf ear to these pleas. Officials at the Department of Marine and Fisheries held fast to the English-speaking world's cultural opposition to commercial applied science (Lucier, 2012): fisheries science to determine the racial characteristics, demographics, geographical distribution, and fluctuations of commercial fish was "pure" and deserved support. But demonstrating new fish-processing methods for commercial ends, no matter how scientific the spirit, was not the proper role of scientists. Desbarats even squashed Hjort's later attempts to carry out in Halifax demonstrations of superior salt-cure methods (Hjort, 1915c, 1915e; Desbarats, 1915).

Ironically, while Canadian civil servants were unimpressed by Hjort's practical approach to fisheries problems, he had the opposite impact on the scientists with whom he interacted. The Department of Marine and Fisheries gave an annual allocation to the Biological Board of Canada to run its Pacific and Atlantic Biological Stations, with no proviso other than that at least some of the volunteer scientists devote time to practical fisheries problems. Later, after the First World War, scientists at these stations began investigating fish-processing problems; in 1919 Archibald Patterson Knight (1848–1935) took on the problem of deterioration in canned lobsters, for example, developing improved canning methods he helped to disseminate among Atlantic Canadian lobster canners. Knight became the Board's Chair in 1921 and reoriented it in a more practical direction. Hjort inspired Archibald Gowanlock Huntsman (1883–1973), the young curator of the Atlantic Biological Station, to incorporate fish-processing problems into the station's programme; Huntsman, with the support of the Halifax Board of Trade, and Knight as the Biological Board's Chair, created a new research station in Halifax dedicated entirely to fish-processing issues. The Fisheries Experimental Station was inaugurated in 1924. A sister station for fish-processing research, the Fisheries Experimental Station (Pacific), was also established in British Columbia in 1924 (Hubbard, 2006; Stewart and Safer, 2005).

Biological Board scientists took up this aspect of fisheries science too late to help Canadian troops in the First World War, who were condemned to rations of Canadian frozen fish—oozing water, with a cardboard-taste and texture—but they made great strides in improving Canadian products during the 1920s and 1930s. Huntsman himself took up the problem of fast-freezing fish so as to leave it in a near-fresh state once cooked: his "Ice Fillets" were a hit on the Toronto market in 1928, and beat Clarence Birdseye's development of a similar product to the market by 1 year. The Department of Fisheries, however, disallowed the scientists from marketing their product after the initial experiment, as it did not want to be seen as competing with private industry. Frozen fish remained a product before its time, however, until refrigeration technology became widespread after the Second World War. Huntsman, while developing flash-frozen fish, also addressed a problem he was encountering in existing refrigeration technology, and invented "jacketed cold storage": this new freezer design sealed the coolant pipes behind steel plates, and became standard in North American railway refrigeration cars (Hubbard, 2006).

Hjort, despite being thwarted in carrying out fast-freezing demonstrations, inspired a flowering of Canadian practical research to improve nets and gear and fish-processing techniques. The Department of Marine and Fisheries's opposition to his holistic programme proved to be no barrier to Hjort promoting the importance of this work to his receptive Canadian scientific hosts and disciples.

Hjort and the Canadian fisheries expedition in 1915: biology and oceanography

Hjort's 1910 and 1914 surveys had pointed to the possible existence of several herring races in the waters of Canada, New England, and Newfoundland. Once back in Norway in January 1915 he proposed to return to Canada to conduct a sea-going expedition in the waters between Newfoundland and the Atlantic Provinces and into the Gulf of St Lawrence. He outlined a number of questions: did growth rates vary in herring from different coastal waters, or by race? Did herring stock fluctuations mirror those of European herring? Where were exploitable concentrations of herring located? He would require two sea-going vessels equipped with Norwegian purse-seines and driftnets and other scientific equipment, to carry out a series of three hydrographic cruises, one each in May and June and a final cruise at the end of July and beginning of August; one ship would focus on the Gulf of St Lawrence, the other would make stations to the east of Nova Scotia, and north to Newfoundland. Both would search for spawning grounds and document growth, migrations, fish distributions, water conditions, plankton, etc. Each cruise was to follow the same course to enable comparisons of conditions (Hjort, 1915a). He wished to have the help of Dr Paul Bjerkan, Hjort's long-time assistant and collaborator, and of an experienced Norwegian herring captain, Thor Iversen, captain of the Norwegian Board of Fisheries' ship "Michael Sars" since 1902.

These proposals were eagerly supported both by Prince and Macallum at the Biological Board and by Canadian fisheries technocrats. Individuals such as J.J. Cowie, the Chief Inspector of Fisheries, hoped that if the expedition found evidence for commercial concentrations of fish stocks in areas off Nova Scotia and between Newfoundland and the Maritimes, that the Maritime fishing industry would abandon its antiquated, traditional fishing techniques and develop offshore fishing capabilities using more efficient technologies (Mills, 2009).

The quickly-approved Canadian Fisheries Expedition disappointed Hjort only in his inability to demonstrate superior fish preservation methods. Nevertheless, while in general the expedition accomplished its scientific objectives, there were several set-backs. The hydrographic equipment was delayed in arriving from Norway due to the war (Hjort, 1915b). The late arrival of spring and ice conditions led to a delayed start to the hydrographic and fisheries surveys, as did the death a commander of one of the survey ships (Hjort, 1915d). The primary vessels used were the Halifax-based Canadian Government Ship (CGS) *Acadia*—which the Canadian Hydrographic Survey had commissioned in 1913, and loaned to the expedition—and the Canadian Coast Guard steamer *Princess*, a former fisheries cruiser purchased in 1906. *Princess* was to be based out of the expedition headquarters in Souris, Prince Edward Island. *Princess*' commander, William Wakeham (1844–1915), an experienced Canadian fisheries inspector, had led several expeditions into the Hudson Bay beginning in 1897; acting for the Canadian government he had proclaiming Canadian sovereignty over Baffin Island and the Arctic Archipelago in 1897. Officially retired in 1909, he returned to duty at the Canadian government's request (Mimeault, 1998). Unfortunately, during the first cruise of *Princess*, he became seriously ill; refusing to end the work, in the end he collapsed, and the cruise was cut short to bring him home to the Gaspe (Hjort, 1915e), where he died on 20 May. Because of these delays and set-backs, only two of the proposed cruises for the Gulf of St Lawrence were carried out.

The cruises were staggered: *Princess* had begun its aborted trip in the Gulf of St Lawrence on 10 May. Hjort embarked on the *Acadia* on 29 May for a fast survey that ended on 4 June. *Princess* conducted its first proper survey from 9 to 15 June, followed by *Acadia*'s second cruise from 21 to 29 July. Finally *Princess*'s second cruise was from 3 to 12 August. Additional information and samples were gathered by the Canadian government's herring "steam drifter" *33* which conducted experimental fishing in the Gulf of St Lawrence. James Playfair McMurrich supervised a 10-day expedition on the Biological Board's small research vessel, *Prince*, in the Bay of Fundy. Altogether, *Acadia* and *Princess* made 162 stations (Figure 1), and *Prince* made 9 stations. Hjort (Figure 2, with *Acadia*'s Captain Robson to his right) assisted by Canadian and Norwegian scientists, measured hydrographic

Figure 1. Hjort and Captain Robson aboard Acadia, Canadian Fisheries Expedition 1915.

conditions and took samples of water, plankton, food fish eggs, and larvae, in the hopes of linking local oceanographic features with fish productivity. With Hjort's leadership, this was the first such work conducted under Canadian auspices, involving Canadian scientists, in Canadian waters. Hjort directed the initial preparation and collation of samples at the two-story wooden house set up as a laboratory in Souris, Prince Edward Island. His assistant Paul Bjerkan titrated water samples to determine salinities, using standard water samples from the ICES Central Laboratory in Copenhagen to calibrate the measurements. Huntsman and Dr Arthur Willey (Chair of the McGill University zoology department) did preliminary work on the plankton and fish eggs samples, but Hjort found the equipment in the temporary lab to be too primitive for its successful completion (Hjort, 1915f). The preserved biological material was mostly worked up by Canadian and Scandinavian scientists in university and fisheries biology laboratories after the expedition's completion.

The Canadian Fisheries Expedition's final report had a tortuous preparation and was not published until 1919, after the war, as materials and drafts had to criss-cross the Atlantic. Challenges arose in part because it was prepared by a combination of Norwegian experts and two Canadian neophytes. Huntsman wrote two of the nine "memoirs", one on herring growth in the Bay of Fundy and one on a quantitative and qualitative study of eastern Canadian plankton. Willey prepared a report on the copepods obtained in the Gulf of St Lawrence and adjacent seas. Unfortunately, an American participant, James Mavor, could not complete his cod growth studies before the 1919 report was published.

A glaring flaw in the publication is that each report was seemingly prepared without knowledge of information in other reports, and Hjort failed to synthesize the material in his overview. The expedition had used methods developed by plankton expert H.H. Gran of the King Frederik's University in Kristiania (Oslo), and the material was turned over to him for analysis. He wrote the report on the productivity of Gulf of St Lawrence and adjacent waters. Hjort turned over the herring year class and population structure work to his assistant Einar Lea, although he did assist Lea in examining scale rings to measure the age of the fish sampled, and taking biometric measurements to distinguish different herring races. Lea wrote the report. Fish egg and larvae samples were handed to Alf. Dannevig, Hjort's colleague who managed the Flødevigen Utklekningsanstalt fish hatchery in Norway. Dannevig's 'memoir' on this subject was probably among the most puzzling of the contributions. While the samples indicated billions of cod eggs and other gadoid eggs being present in the Gulf of St Lawrence, there were very few larvae of these species. For Hjort this raised a problem: why would so many cod spawn in a region in which billions of eggs would be doomed for destruction? With no material from other years for comparison with the 1915 samples, he could not determine if this was an anomaly, but the questions raised certainly showed the urgent need for more surveys and sampling (Hjort, 1919).

For the hydrographic work, no Canadian was competent to analyse the samples and data or write the report. Therefore, Paul Bjerkan reported on hydrographic observations and salinities, while J.W. Sandström, a Swedish pioneer of the new dynamic oceanographic approach that later revolutionized physical oceanography in the twentieth century, reported on the region's currents, water movements, and hydrography. His report included a 46-page introduction to the new dynamic oceanography that, according to historian of oceanography Eric Mills, he intended to serve as a basic training manual for Canadian oceanographers (Mills, 2009). Einar Lea's "Report on the 'Age and Growth of the Herring in Canadian Waters'" similarly began with a 39-page discussion of Lea's scale-ageing methods, also most likely intended to proselytize the methods developed by ICES scientists and to serve as a beginner's manual for Canadian scientists interested in using these methods (Hubbard, 2006).

The consequences for Canadian fisheries science

Perhaps Hjort's most important objective in undertaking the Canadian Fisheries Expedition was to introduce ICES-style fisheries biology to Canada; this truly international expedition—with the above-mentioned experienced professional participants from Norway and Sweden assisting those from Canada and the United States—served as an intensive training course for the North American participants, whose approach until then resembled natural history studies of the nineteenth century. The Canadian participants, who in effect became Hjort's students in an intensive fishery biology "course", included Huntsman and McGill University embryology professor Dr Arthur Willey (who much earlier completed his doctorate under the tutelage of E. Ray Lankester), and University of Toronto anatomy professor James Playfair McMurrich (who later became Chair of the Biological Board of Canada). His American collaborator and student was James W. Mavor, a Harvard graduate who served as Atlantic Biological Station curator in 1913 and 1917, and who soon after the expedition became a professor at Union College in Schenectady, New York. After the expedition, Mavor worked on problems of fish growth and hydrography during summers at St Andrews, abandoning his earlier parasitology research (Hubbard, 2006).

Among the quantitative methods Hjort introduced were those developed in the previous 15 or so years by German scientists: Dr Friedrich Heincke's approach to distinguish fish races using biometric measurements such as fin ray counts, vertebrae counts, and other measures; C. Hoffbauer's method of counting growth rings on scales to determine fish age; Johannes Reibisch's use of vertebrate and otolith growth rings for the same purpose; and his own use of a combination of these, in tandem with fisheries statistics, fish population vital statistics, and studies of fish migration. His educational

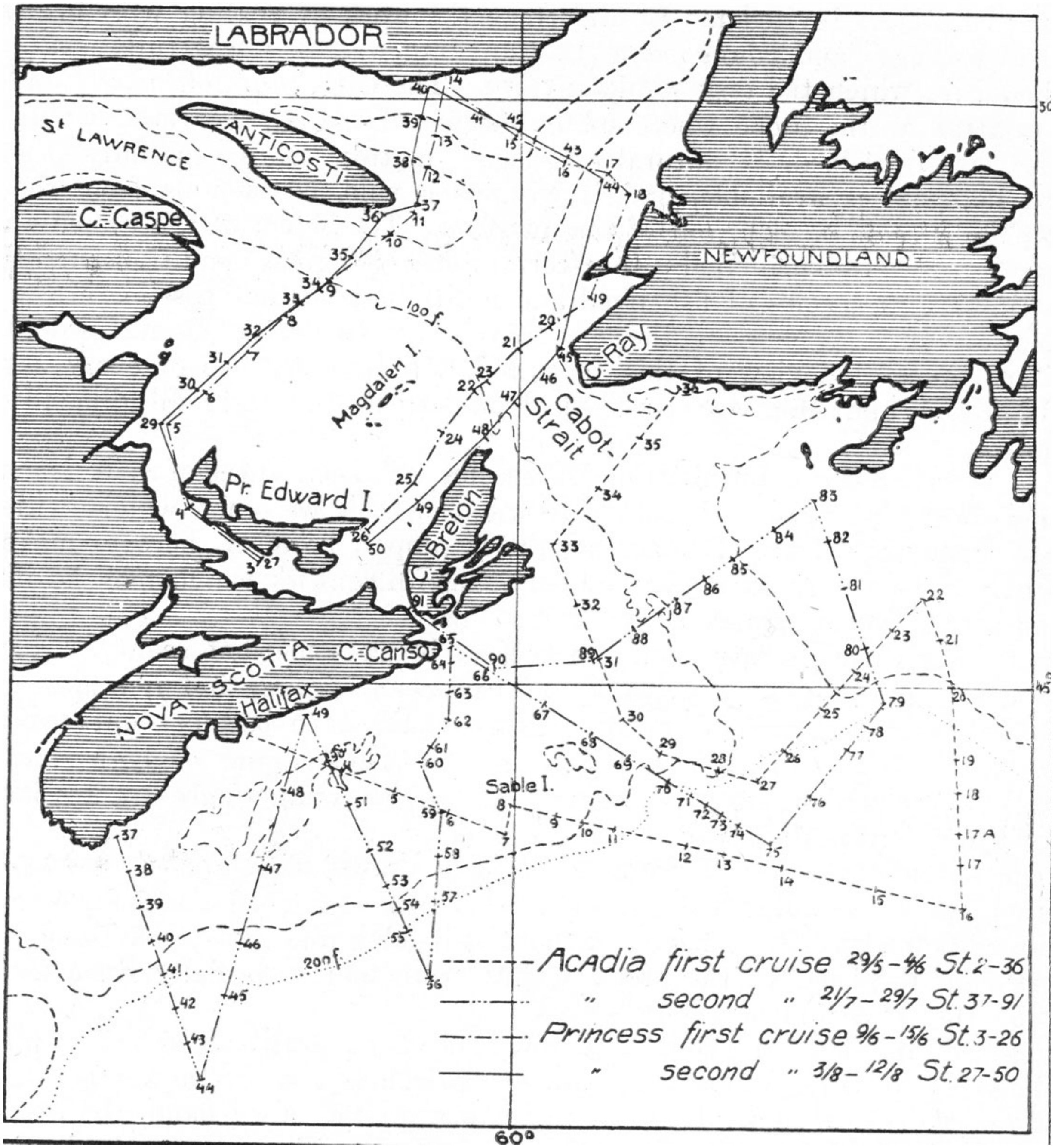

Figure 2. Cruises and stations of Princess and Acadia, May – August 1914.

goal was a familiar one for Hjort. As a scientist from a small nation, Hjort shared the eagerness of other Norwegian natural scientists to participate in Scandinavian and international collaborative research, as the quality of their science was highly dependent on their ability to partake in exchanging data and discussing, presenting, and diffusing their results internationally. Through ICES, Norwegian marine scientists could rapidly spread their methods, new instruments, and results from ongoing research; they also organized annual 2-month courses in Bergen from 1903 until 1913, and trained roughly 175 participants (Schwach, 2000).

Hjort's most important Canadian student was Huntsman (Figure 3), who until his first encounters with Hjort in November, 1914, had made ascidian taxonomy his research focus. Huntsman, newly appointed as the Atlantic Biological Station's first permanent curator—and who was in 1916 to become its first full-time director—was chosen by Prince and Macallum to assist Hjort in working up the scale samples from Hjort's travels from New England to Newfoundland. Huntsman immediately spied a flaw in this method—and exasperated Hjort by pointing out that "the scales could not be growing proportionately to the whole fish, since in the small herring, of which [he] . . . had one preserved in a bottle, the scales did not touch each other, while in a large herring, they overlapped greatly" (Huntsman, 1951). Annoyed, Hjort declared Huntsman unfit to work with scales; Huntsman nevertheless became Hjort's primary Canadian assistant during the 1915 expedition. Hjort switched Huntsman to counting vertebrae and studying plankton, and introduced Huntsman to the basics of European fish population analysis, plankton studies, and hydrography, the main components of ICES research. Despite their initial clash, both held each other in great respect and corresponded on various issues for the rest of Hjort's life. His encounter with Hjort led Huntsman to abandon ascidian taxonomy and embrace all aspects of fisheries biology. Within 3 years after the expedition, he published articles on methods in fisheries biology (Huntsman, 1918a), hydrography (Huntsman, 1918b), and the fish scale method—with proposed improvements (Huntsman, 1918c). He also published the world's earliest mathematical model of showing the effects of fishing on fish populations size and age structure (Figures 4 and 5). His graph showed the shrinking numbers of older year classes, and comparative expansion of young fish in fished populations (Huntsman, 1918d). Unfortunately, this analysis appeared in the Biological Board's first *Bulletin*, directed at fishers, and escaped wider scientific attention at that time. Nevertheless, fisheries biologist and historian Tim. D. Smith believes that Huntsman's ideas influenced W.F. Thompson's epochal work for the Pacific Halibut Commission in the 1920s and 1930s (Smith, 1994), and his re-analysis of this material in the late 1940s had important influences on later theory of fishing population models (see Hubbard, in press). Huntsman continued to teach during the fall and winter as a tenured professor at the University of Toronto after being hired as the Biological Board of Canada's first full-time fisheries biologist and director of the Atlantic Biological Station in 1915. Although he was not paid by the University of Toronto, his position there enabled him to train a generation of Canadian graduate students as fisheries biologists; Hjort, through Huntsman, was therefore instrumental in the new discipline's emergence as a leading scientific sector in Canada.

Figure 3. Archibald Gowanlock Huntsman, the Canadian scientist who adopted Hjort's and ICES' methods and who trained subsequent generations of Canadian fisheries biologists and promoted Canadian oceanography.

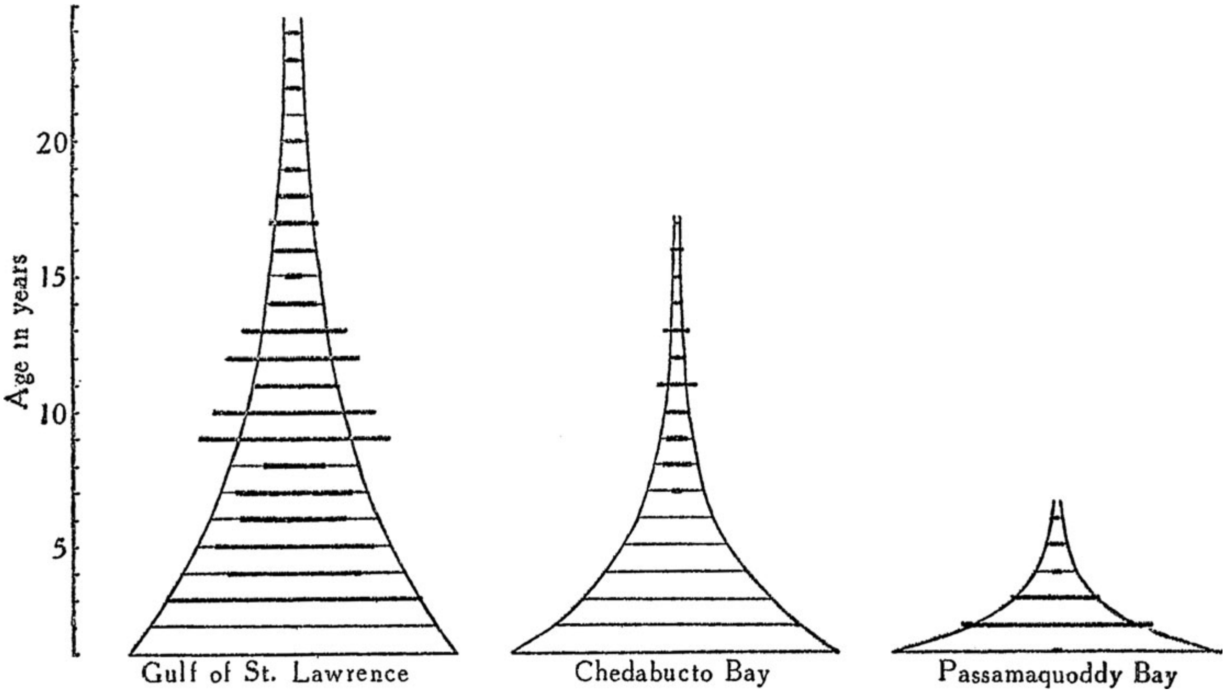

Figure 4. Huntsman's graph showing the age structure of unfished plaice populations in three regions around the Maritime Provinces.

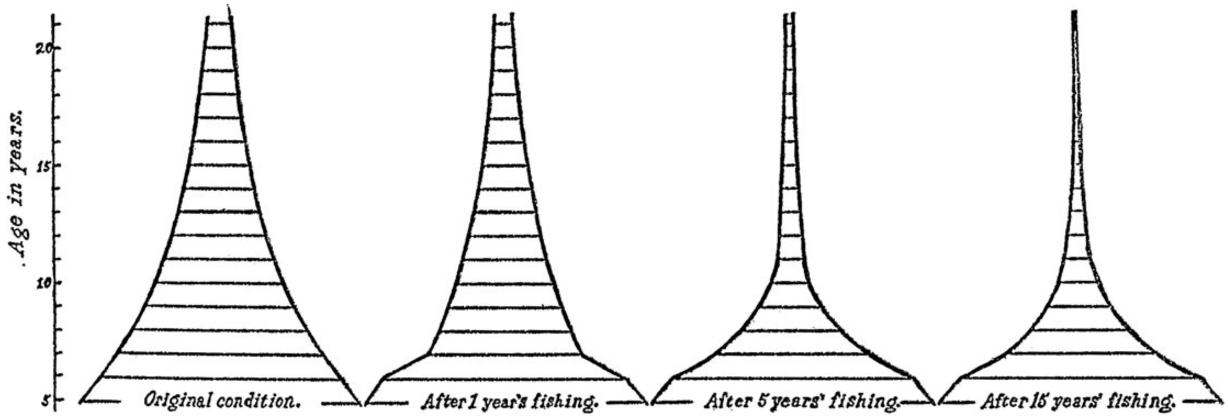

Figure 5. Huntsman's graphical representation of the effects of fishing on Maritime plaice populations.

International networks

Beyond the lasting changes that Hjort wrought through launching the new ICES-developed version of fisheries research in Canada, his enthusiasm for the project had another vital outcome, in the shape of the many lasting linkages he forged between American, Canadian, and Norwegian scientists. One of these connections was an accident of war. Wartime hostilities delayed the Atlantic crossing of Captain Iversen and the Norwegian hydrographic and fisheries equipment. Hjort, searching for alternative gear, turned to Dr Henry B. Bigelow (the future founding director of the Woods Hole Oceanographic Institution), who was then engaged in hyrographic and fisheries investigations in the Gulf of Maine for the United States Bureau of Fisheries. His gear was housed at Harvard University between research seasons, and Hjort, accompanied by his wife, set off to meet Bigelow and arrange to have the gear sent north. Tremendously impressed by Bigelow, he lingered for a few days to learn about conditions off Nova Scotia, which had been the focus in 1912 and 1913 of hydrographic surveys—including the earliest American quantitative plankton sampling, using Victor Hensen's methods—by Bigelow and the US Bureau of Fisheries (Hubbard, 2006). Bigelow's and the Biological Board's resulting mutual awareness was to blossom into close ties in the early 1920s, when Huntsman helped instigate the formation of the North American Council on Fisheries Investigations (NACFI); and Bigelow and Huntsman both served as scientific representatives and officers for this organization. Huntsman and Bigelow had many arguments about oceanography and fisheries science in their resulting spirited correspondence, and a lifelong friendship arose.

Hjort also had to call upon other Norwegian and Swedish scientists to help write the reports, as Canada at that time lacked experts capable of preparing reports according to the latest methods. New dynamic oceanographic methods had been developed in Norway by Vilhelm Bjerknes (1862–1951), and made practical by Bjørn Helland-Hansen (1877–1959) and Johan Sandström (1874–1947). Therefore, Bjerkan, Hjort's assistant, and Sandtröm were brought in to report on the Canadian Fisheries Expedition's hydrographic work. Hjort also appointed the professor of botany at the University of Oslo, Haaken Hasberg Gran (1870–1955), to work up and report on the plankton collections. Huntsman and Bigelow in the early 1930s were to hire Gran and his student, Trygve Braarud (1903–1985) as his assistant, to come to St Andrews and work as plankton experts for the International Passamaquoddy Fisheries Commission in 1931 and 1932—a scientific commission appointed by NACFI for the Canadian and US governments to determine the environmental effects of building hydroelectric tidal-power dams between Passamaquoddy Bay and the greater Bay of Fundy.

Hjort, then, through his dynamic and extrovert personality, forged ties between Canadian, American, and Scandinavian scientists who were to influence the course of fisheries biology. His influence in Canada, in this respect, was especially important as it drew Canadians beyond their traditional British, and occasionally American, scientific role models and into a wider international community.

Conclusion

Unfortunately for the Canadian government, poor economic conditions, not lack of fish, were holding back the fisheries' economic development: the Canadian Fisheries Expedition was a complete failure if measured by its immediate consequences for the Canadian Atlantic fisheries. For Hjort, one of the great rewards from leading the Canadian Fisheries Expedition was having his year-class theory further vindicated. The survey's experimental fishing and sampling revealed strongly dominant year classes: in the waters off Newfoundland, as in North Atlantic waters closer to Europe, this was the 1904 year class. One finding particularly pleasing to Hjort was that each of the four "races" or distinct groups of herring identified seemed to have a unique pattern of year-class abundance, reinforcing his theory that there were different "tribes" of herring; the 1903 and 1908, 1909–1910 year classes dominated in herring in Nova Scotian and Bay of Fundy waters. For Canadian fisheries biology, the Canadian Fisheries Expedition's results were dramatically more important. In the wake of this expedition, several researchers, especially Huntsman, were motivated to adopt the ICES approach to fisheries studies, though limited by small research vessels and limited equipment and funding. Huntsman was profoundly influenced by the demonstrated importance of studying oceanographic conditions to understand how these affect fish populations. It was due to his insistence and persistence that Canada's first full-time oceanographer, Harry B. Hachey, was hired to work at the Atlantic Biological Station in 1928 (Mills, 2003). Huntsman led several smaller expeditions in the Bay of Fundy, Annapolis Basin, the Miramichi estuary on the Northern New Brunswick coast, and Gaspé region during the following years (Figure 5). These culminated in one major international expedition, the Strait of Belle Isle Expedition, in 1923, under the auspices of NACFI, with British, American, and French participation. As increasing numbers of Canadian researchers and even some US researchers fell under Huntsman's sway, the stamp of ICES fisheries research was apparent in the annual and long-term research programmes being fielded by the Biological Board of Canada, reflected in the organization's name change to the Fisheries Research Board of Canada in 1937. International networks were formed as scientists across the Atlantic and across nations sought to investigate and understand the resources of the borderless oceans. Hjort and his Canadian Fisheries Expedition transformed, permanently, Canadian fisheries biology and oceanographic science and made it a part of a global marine science enterprise that he also helped to create.

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Handling editor: Howard Browman

ICES Journal of Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2008–2011. doi:10.1093/icesjms/fsu152

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food for Thought

The graceful sigmoid: Johan Hjort's contribution to the theory of rational fishing

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Holt, S. J. The graceful sigmoid: Johan Hjort's contribution to the theory of rational fishing. – ICES Journal of Marine Science, 71: 2008–2011.

Received 12 August 2013; revised 14 August 2014; accepted 14 August 2014; advance access publication 8 September 2014.

This historical essay describes the theory behind, and implications of, models of optimum yield from an exploited animal population (in particular for whaling) formulated by Johan Hjort and his colleagues, Per Ottestad and Gunnar Jahn, in the 1930s. The essay places the evolution of fishery science during the 1930s–1940s into context.

Keywords: cod, growth overfishing, herring, maximum sustainable yield, Michael Graham, optimum yield, recruitment overfishing, size and age composition, surplus production model, whaling.

Johan Hjort is widely known and honoured for his immense contributions to oceanography and fisheries ecology. He is less well known for his seminal role in promoting the application of science to whaling and the conservation of the great whales. I hope to correct the balance.

The first formal international agreement on the conduct of whaling, including a number of regulations intended to limit or control commercial whaling, was negotiated in 1931 under the auspices of the League of Nations in accordance with an initiative launched in 1926 by the International Council for the Exploration of the Sea (ICES). The first important move in August 1929 under the ICES initiative was the appointment of an International Statistics Committee (ISC) chaired by Gunnar Jahn, Director of the Norwegian Statistical Bureau, with Sigurd Risting, Secretary of the Association of Whaling Companies (AWC), and Johan Hjort as members. Risting was effectively the founder of the Bureau of International Whaling Statistics. He had been collecting whaling statistics on his own since the end of the 19th century, completing them, as far as was possible, back to the beginning of "modern whaling" in 1868 (i.e. using steam catcher boats, bow-mounted cannons, and a harpoon with a grenade head). In addition, as Secretary of the AWC, he had as early as 1919 asked the Directors of the whaling companies to ensure that the lengths of all whales killed in the Antarctic were measured, including the sizes of foetuses in the pregnant females.

Hjort served on the ISC until 1939 when he resigned. During the 1930s, Hjort was the scientific brain behind the construction of the best international database ever assembled on whale fisheries. Interest in whaling was not a side line. The catching and processing of the largest baleen whales—blue, fin, humpback, and sei—was by far the biggest Norwegian fishery in terms of sheer quantity and economical importance of all Norwegian fisheries during the inter-war years. This fact has been obscure simply because whale catches were always recorded as numbers, not weights, and the significance of the records of quantities and prices of products from the whales was not always noticed.

The whaling database was remarkable, especially because it recorded not only catches but the whaling effort, biological information about whales, the details of the whaling fleets, the quantities and values of products and some other economic data, particularly about whale oil. The information was collected by national inspectors on whaling factory ships. Thus, by the beginning of World War II, Hjort and his colleagues had a fairly good idea of the states of the populations of the whales that migrated to and from their Antarctic feeding grounds, which were targeted by the whaling industry. They based their assessments on changes in relative abundance (derived from catch-per-unit-effort data), size compositions, proportions of mature and immature animals, sex ratios, longitudinal and limited latitudinal movements within the Southern Ocean, the timing of migrations and growth of the whales during the feeding season.

Hjort's work concerning whales and whaling was not limited to the interpretation of statistics. The Norwegians and British were already cooperating in an extensive tagging programme with the standardized *Discovery* tags that were retrieved from the blubber during the flensing process on board the factory ships, and from the boilers used to extract the oil, also on board. The recording tag returns was also the responsibility of the national inspectors, occasionally helped by scientists who participated in the long, arduous voyages. The other research interest was in methods of estimating the ages of dead whales, which Hjort knew, from Norwegian fisheries research on herring and cod scales, was of critical importance if science-based management measures were to be taken.

British researchers—mainly—were using the number of *corpora lutea* in the ovaries of killed mature females to get a grip on age. There was one corpora lutea per pregnancy, but these numbers could not, of course, be converted to absolute ages without knowledge of the frequency of pregnancy (thought to be one every two years) and the age at sexual maturity. However, if the time between pregnancies could be estimated accurately, then they could be used as indicators of age composition of catches and, hence, total mortality rates. Hjort and his colleagues in Norway were focused on determining the ages of young animals (up to 3–4 years) from grooves (striations) on the baleen plates.

Hjort knew from studies of the ages of herring and cod that large variations in annual catches could be attributed mainly to natural variations in recruitment. And ageing studies had also shown that fish grow fastest when they are small, and that growth continues, but at a decreasing pace, throughout their lives. This gave strong support to the fisheries inspectors of the late 19th century, such as Ernest Holt and Frank Buckland, who had argued that more fish should be given the chance to grow bigger and become more valuable by reducing the intensity of fishing operations. Age determination provided the means by which this theory could be quantified and tested.

In 1933, Hjort published a seminal paper on what later became called "The Theory of Fishing". It was co-authored by Gunnar Jahn and Per Ottestad and published in a special issue of a scientific journal largely devoted to studies of whales (Hjort *et al.*, 1933a). That issue, entitled *Essays on Population*, contained three other papers: one by Hjort *et al.* (1933b) on Norwegian pelagic whaling in the Antarctic; another entitled "Introductory Remarks" by Hjort on whales and whaling (Hjort, 1933); a paper by Ottestad on "The Mathematics of Growth" (Ottestad, 1933) and one by Alf Klem on experiments on the growth of cultivated yeast populations (Klem, 1933), a far cry from whales in size, but a useful subject for population modelling.

Hjort *et al.* (1933a) developed the notion of an "optimal catch" at some intermediate intensity of exploitation. They did this mainly in relation to the exploitation by Norwegians of the fin whales found off the coast of Iceland, but they also looked at the fisheries for spawning herring and cod landed in Norway and the English trawl fishery for plaice in the Southern North Sea. Hjort and his co-authors used age-distribution data for the cod and herring—from scale rings. For the whales, they used a proxy for age—the proportions of juvenile (0–1 group), immature (2- to 3-year-old group) and mature individuals in the catches. They took a similar approach to the study of plaice, referring to the market categories "large" and "small"—i.e. older and younger fish.

Eventually, Peter Purves, at the British Museum in London, resolved the ageing problem in baleen whales by reading rings in the waxy ear plugs, although the frequency of these rings—one or two per year—remained unclear until the late 1960s. An incorrect assumption that the calving interval was only 1 year distorted assessments of whale stocks until then (Purves, 1955; Gabriele *et al.*, 2010).

Scientists and authorities have usually discussed whales in terms of population numbers, not weight (biomass). There is a good reason for this: they are not easily weighed. Even length measurement when alive is difficult and unreliable. However, they have always been valued commercially in terms of the weight or, with respect to oil, the volume of products. The focus on numbers instead of weigh has important implications in terms of managing whaling and recovery of depleted populations. In the 1970s, IWC scientist proposed regulations to restore depleted stocks in terms of weight, but the whaling industry resisted. Presumably, they knew that a depleted stock, if protected to allow recovery, takes much longer to reach an optimal sustainable weight than merely to recover numerically, especially considering that whales may live for a century and, like fish, they have indeterminate body growth.

Very soon after the Hjort and Ottestad work, Michael Graham published his "Modern Theory of Exploiting a Fishery" (Graham, 1935). In 1946, Graham told me that at that time Hjort and he were corresponding to each other and with Gunnar Rollefsen in Bergen, and also meeting each other in the ICES context. Graham's "theory", which he applied to North Sea cod and plaice, was similar to Hjort's but with a certain difference. Hjort's sigmoid curve was derived from the interaction between mortality—through change in the size/age composition of the catch—and reproduction; the birth rate. Graham's, on the other hand, was based on the interaction between a mortality rate and the rate of growth in body size. Reproduction, through a relatively constant annual recruitment, played no part in Graham's theory, essentially because no relationship between the number of spawners and the resultant recruitment could be found. Conversely, it is not surprising that whales demonstrate a strong stock–recruit relationship, considering their much lower reproduction rate and the long period of maternal care for their young offspring.

Graham viewed the sigmoid population growth curve as possessing a sort of magic Graham (1939), and he once told me that he conveyed this idea to Hjort and to Rollefsen. In his remarkable book, "The Fish Gate", Graham credits Hjort with the opinion that "there is something here that has very wide application, in Nature and in human endeavor" (Graham, 1943, p. 172). Like D'Arcy Thompson before him (Thompson, 1917), Graham saw the shape of this relationship as typical of natural biological processes as opposed to the human-generated shapes of circles and straight lines found in mechanical devices and constructions. William Hogarth had described the sigmoid in his *The Analysis of Beauty* (1753) as "the serpentine curve that swings both ways". With similar thoughts, Graham saw the so-called Gothic arches in architecture as essentially "organic". Aesthetics aside, the original inventors saw the "magic" of their new arches in their extraordinary strength. However, it may be that the significant feature of the sigmoid function is the existence of an inflexion and, hence, an intermediate reference point.

A decade later, Milner Schaefer used Verhulkt's symmetrical logistic population growth curve as the basis of his very different theory of fishing (Schaefer, 1953, 1954, 1955a,b), now usually referred to as the Surplus Production model—a term borrowed from Karl Marx's "Surplus Value" theory of political economy—in which it is assumed that sustained biological productivity, and hence potential catch, is a simple linear—or, later, as developed by

Schaefer's associates Pella and Tomlinson (1969), a more flexible power function of population biomass, regardless of the size and age composition of that biomass. Schaefer had to ignore age composition because there was at the time no way of determining the age of an individual tuna (he was studying the yellowfin in the Eastern Tropical Pacific, although he had published similar ideas with respect to the Pacific halibut 1954).

Some recent authors (notably Quinn and Deriso, 1999, following Smith, 1994) have erroneously conflated the Graham/Hjort idea with that of Schaefer, referring to the logistic curve—which Schaefer also supposed could equally apply to population growth in weight as to the growth in number—as the "Schaefer/Graham" procedure (Graham considered the curve of population growth in weight as being sigmoid but did not apply the logistic expression to it).

The matter of the importance of the inflexion of the sigmoid as a guide to fisheries management was implicitly a subject of considerable controversy at the United Nations' (UN) Technical Conference on the Law of the Sea held at the Headquarters of the Food and Agriculture Organization in Rome in 1955 and it had political repercussions in the first UN Law of the Sea Conference, held in Geneva in 1958. Maximum surplus production (which is equivalent to Maximum Sustainable Yield, MSY) that corresponded to the inflection point according to Schaefer's model was advocated as a global objective for fisheries. In private correspondence (of which copies are in my files and the archive of Schaefer's papers), Graham vigorously rejected Schaefer's approach to both assessment and management and dismissed his request for co-authorship. In controversial arguments about "surplus production" models, a basic fact was generally overlooked: the Schaefer version of the logistic model was derived from an assumption about density dependence, but there was no explicit density dependence in either Hjort's model (mortality rate vis-à-vis a constant-specific rate of reproduction), or in Graham's interaction between a constant mortality rate and a constant sigmoid curve of body weight against age. Body growth of whales came into the Hjort *et al.* story only by virtue of size being an indicator of approaching sexual maturity.

Neither Hjort nor Graham knew in the 1930s about the paper by Baranov (1918) that provided a formal algebraic description of a population model—but only in Russian and at a politically inconvenient time of civil war, revolution, and foreign invasions aimed at St Petersburg, where Baranov was based. A translation in English by the Canadian scientist W. E. Ricker was circulated outside the USSR only towards the end of the Second World War. Unfortunately, Baranov incorporated a linear body growth equation in his formula instead of a sigmoid one with an upper asymptote (such as those by L. v. Bertalanffy and by B. Gompertz—see Quinn II and Deriso) which was a serious flaw in an otherwise innovative approach. Ricker (1940) and Hulme *et al.* (1947) later made similar errors, especially Ricker who assumed exponential body growth. The result is a distortion of stock weight by the inclusion of a very small number of enormously old animals in catches: Ricker and Hulme *et al.* corrected this by simply truncating their age compositions. Thompson (1937; 1950) and Thompson and Bell (1934), made no such mistake; they applied an empirical series of yearly fish weights in their rather similar calculations, but eventually Ray Beverton and my use of the von Bertalanffy expression became almost universally applied in fish stock assessments.

All fishing, including whaling, is selective with respect to the size and age of animals taken, and it has long been known that exploitation changes the size and age composition of the stock. Hjort and Graham were well aware of this and their approaches permitted some account to be taken of that phenomenon and the consequences of changes in selectivity. Schaefer and his followers, applying the surplus production theory, were unable to do that. The models by Beverton and me in the 1950s generalized this matter.

The International Convention for the Regulation of Whaling, 1931 (*The Geneva Convention*), negotiated under the auspices of the League of Nations, prohibited "the taking or killing of calves, suckling whales, immature whales and females accompanied by calves". In reality, gunners could not tell whether a whale was mature or immature before they had killed it. As time went on, and the stocks declined and the average size—hence average age—of animals in them diminished, the relative frequencies of mature and immature animals in catches changed. Hjort and his colleagues were, therefore, concerned about what Cushing (1972) later defined as *recruitment overfishing*.

Graham and his collaborators were, on the other hand, concerned essentially with the consequences of the interaction between mortality and body growth, and Cushing's *growth overfishing*. They mostly favoured increasing the mesh sizes of the codends of otter trawls. There was little if any evidence at the time (despite much argument and speculation) that fishing was affecting the numbers of annual recruits of teleost fish to the major stocks. The underlying implicit assumption was that there is extremely strong density-dependent mortality (effectively infinite) in abundant pre-recruit life history phases.

At the beginning of the 20th century Ernest Holt and others had advocated allowing fish the chance to spawn at least once; this idea is to be found in several official reports—especially in the UK Parliament—during the second half of the 19th century, but this idea did not come from an expectation that effective reproduction was being affected; the idea was essentially to allow fish to grow bigger than they otherwise would. Fish generally attain maturity when they reach between ~25 and 37% of their theoretical asymptotic weight, near the inflexion somewhere along one of the sigmoid *Generalised Logistic* curves postulated by Richards (1959). For the now commonly used von Bertalanffy (essentially a cubic) version, this would be at 0.3 of the asymptote, and for the Gompertz or Fox equation, an exponential version, this is $1/e = 0.37$ of the asymptote.

A consequence of the combination of exponential mortality and sigmoid growth is that the total weight of a cohort (a single year class of fish) usually increases as it gets older, then declines as continuing mortality "overcomes" a slowing growth rate. The point at which this happens is called the *critical age* and *size*, and the maximum total weight the *critical weight*. I think it was Herrington (1943) and Nesbit (1943) who first noticed the significance of the critical weight, which he called the optimum catch. It was discussed by Beverton and Holt (1957, p. 374; although in our jointly authored publication this section was actually written by Beverton). The critical weight of the oldest cohort in the population is, strictly speaking, the MSY from the stock, but it is unobtainable because it could only be secured by catching simultaneously all the surviving members of the cohort, which would require infinite fishing effort.

Herrington's optimum was, in fact, the upper end of the "eumetric" ridge along an isopleth diagram such as Beverton and I constructed, with horizontal axes of fishing rate and selectivity: the ridge itself maps the "local" *MSY*s corresponding to all possible selectivities.

The term "optimum" itself could now be better applied to designate best compromises between two or more alternative measures, policies or parameters, including such as catch rate/profitability, desirable size of fish in the catch, degree of precaution against human error or natural change.

It is of interest that Herrington was science leader of the US delegation in the peace negotiations with Japan in 1947–1951. He pressed for adoption of the "abstention principle" to be applied when a coastal state claimed to be taking the MSY from adjacent waters. Clearly, the USA's interest in embedding Schaefer's MSY concept into international fisheries management persisted.

The need for serious attention to the consequences of selectivity and changes in it became evident when, in the post-WWII years, industrial fishing for "reduction" to oil and meal, in which the size of fish does not matter much, became profitable and technically feasible in many circumstances. Local *MSY*s, and the fishing intensity needed to take them, differ enormously between an industrial fishery and a fishery for mature fish utilizing the same stock. Hence, it was no accident that the first collapse of a large valuable fishery—that for anchoveta off the coast of Peru in the 1950s—was triggered by a virtually infinite foreign market, with minimal production costs (no buildings needed to house reduction plants in the coastal climate of Peru) and a fishing gear that would take baby fish, perhaps aided by changing ocean conditions. Several other collapses were to follow, for similar reasons—and I am not talking about the peculiar diadromous salmons and eels (Myers, 1949), or even the grey mullet which spawns in the sea and feeds in freshwater.

A level of exploitation effort required to obtain any MSY depends critically on the chosen selectivity. "Modern whaling" has, however, practically always been a combination of securing a product suitable for direct human consumption, and production of "reduced" substances such as protein-rich meal and fats and oils. This consideration has never, however, played a significant role in decisions about minimum acceptable sizes of whales to be caught.

Unfortunately, Hjort died in October 1948 and, therefore, did not live to see his, Graham's, E. S. Russell's (Russell, 1931, 1942), Thompson's and Baranov's ideas come into bloom in the 1950s.

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ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2012–2016. doi:10.1093/icesjms/fsu147

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food for Thought

Johan Hjort's impact on fisheries science: a bibliometric analysis

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Aksnes, D. W., and Browman, H. I. Johan Hjort's impact on fisheries science: a bibliometric analysis. – ICES Journal of Marine Science, 71: 2012–2016.

Received 5 August 2014; accepted 5 August 2014; advance access publication 8 September 2014.

We analyse how Johan Hjort's publication, "Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research" (Hjort, 1914), has been cited in the subsequent scientific literature. In the context of this special issue commemorating the 100th anniversary of Hjort's seminal publication, our objective is to provide insights into how his work has penetrated the literature and influenced the development of fishery science. We also tracked Hjort's related article, "Fluctuations in the year classes of important food fishes" (Hjort, 1926). We present the citation life cycles of these articles and analyse various characteristics of the publications that cite them. The importance of Hjort (1914) is reflected in the large number of citations that it has accrued (908), and by the 40–50 citations that it continues to receive every year. This is exceptional for a 100-year-old scientific article, in any field. Hjort (1926) initially received as many cites as Hjort (1914), but the latter subsequently became the paradigmatic article. Hjort (1914) has been cited in 162 different journals and by scientists in 53 countries—Hjort's work has had a broad and global impact on fisheries research. The contextual analysis demonstrated that Hjort (1914) is considered a seminal, novel, and paradigm setting study—the core research questions addressed by Hjort (1914) remain unsolved and several of his hypotheses continue to drive fisheries science to this day.

Keywords: 1914, delayed rise no decline, fish biology, highly cited, recruitment.

Introduction

One hundred years ago, Johan Hjort, in his publication "Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research" (Hjort, 1914), posited an interrelated set of hypotheses that have driven fisheries science ever since—the migration/movement, year-class success, parental condition, prey field ("critical periods"), and dispersal hypotheses. Hare (2014, page xx) states, "Arguably, Johan Hjort is the father of fisheries oceanography. His 1914 publication set the stage for a century of work aimed at understanding fluctuations in abundance of fishery species. Hjort knew that fishery yields varied through time, and his purpose was to understand the basis for this variability". The importance of Hjort (1914) is reflected in the large number of citations that it has accrued, and by the unusually large number of citations that it continues to receive every year (detailed below). The latter is, to say the least, exceptional for a 100-year-old scientific article. Therefore, we herein analyse how Hjort (1914) has been cited in the subsequent scientific literature.

In the context of this special issue commemorating the 100th anniversary of Hjort's seminal publication, our objective is to provide insights into how his work has penetrated the literature and influenced the development of fishery science. We also tracked Hjort's related article, "Fluctuations in the year classes of important food fishes" (Hjort, 1926). We present the citation life cycles of these articles and analyse various characteristics of the publications that cite them. Further, using citation context analysis, we investigate and comment on the reasons why Hjort's work continues to be cited. This article is intended to be complimentary to the more biographically oriented articles about Johan Hjort that appear in this special issue (Hubbard, 2014; Schwach, 2014), as well as with Rice and Browman (2014), who track how "recruitment process" research has been subsumed into research on ecosystem-based management and climate change.

Material and methods

The bibliographic database Web of Science (WoS), Thomson Reuters, was used to trace the influence of Hjort's research in the literature. WoS indexes the majority of the international scientific journals in the fields of fisheries and marine biology. The WoS database is, therefore, well suited to assessing Hjort's impact. However, it is important to note that the standard WoS coverage only extends back to 1945. Thus, the database cannot be used to analyse the research literature in the first three decades after Hjort (1914) was published. It should also be noted that the coverage of the database, in terms of journals indexed, has increased significantly over the course of time—the database presumably covers a larger part of the research literature today than it did in the past (see Aksnes and Hessen, 2009).

Hjort's publications are not indexed as primary literature in the WoS. Therefore, the citations to the articles from the indexed literature were traced using the WoS' citing reference function in which the author names and publication year are used to identify cited references. We searched for citations to "J Hjort, 1914" in journals that are indexed in WoS from 1945 onwards. Therefore, our analysis surely underrepresents the true number of citations and penetration of Hjort (1914). We used the same procedure to search for Hjort (1926), using "J Hjort, 1926". The searches were carried out in January and February 2013.

The retrieved citing publications were then analysed according to bibliographic parameters such as publication year, journal, and nationality of citing authors. In addition, we conducted a citation content analysis in order to explore the reasons why Hjort's publication is still cited in the contemporary literature (see below). In order to make some comparisons with the research output in fishery and marine biology generally, we also used the National Science Indicators (NSI) database which the Nordic Institute for Studies in Innovation, Research and Education (NIFU) has purchased from Thomson Reuters. This database contains aggregated bibliometric data at country and field/subfield levels. The 2012 edition of NSI, with data covering 1981–2011, was used.

A quantitative bibliometric analysis does not yield any information about the reasons why an article or author's work continues to be cited. In order to provide more insights into that question, we conducted a citation context analysis by analysing the textual passages in which Hjort (1914) is referred to in the citing documents (*sensu* Small, 1982). This is very time-consuming as each article has to be examined manually. Therefore, we made an arbitrary choice to look only at citing articles that in turn have been highly cited. Using this approach, we were able to assess the influence of Hjort's work on other high impact publications within the field. We limited the study to articles with 140 or more citations—a total of 41 articles, of which we were able to obtain 37, were examined for content analysis. Thus, the context analysis should be considered illustrative rather than systematic.

We also input the titles of all of the articles in WoS that had cited Hjort (1914) into the www.wordle.net tool and generated a word cloud that illustrates the frequency of occurrence of the words in those titles. Common words that do not have thematic content, such as *and*, *of*, *the*, etc., are excluded.

Results and discussion

In total, 908 unique citations of Hjort (1914) and 187 unique citations of Hjort (1926) were identified (includes citations from 1945 to January 2013). The number of citations has increased with time, with Hjort (1914) currently being cited an impressive 40–50 times per year and Hjort (1926) 5–10 times per year (Figure 1). Very few publications, in any field, attain citation numbers as high as Hjort (1914), and the current citation rate is exceptional for a 100-year-old scientific publication. In fact, from a total of over 120 000 indexed articles in the WoS category "Fisheries", only 7 have accrued a higher total citation count than Hjort (1914).

The typical citation life-cycle pattern of a scientific publication is a parabolic curve of rise and decline. An average article is poorly cited the first year after publication; a citation peak is reached ~3 years after publication, followed by decreasing citedness the subsequent years (Aksnes, 2003). There are, however, differences in citation life cycle across fields; in fisheries research, the rise typically takes longer, although it rarely asymptotes at a level anywhere near as high as Hjort (1914). Moreover, there are also large variations in citation life cycle at the level of the individual article. In a previous analysis of highly cited publications, Aksnes (2003) identified different clusters of temporal citation patterns. One category of highly cited articles, termed "delayed rise, no decline" articles, is characterized by a relatively slow rise in citation frequencies and a stable or increasing citation level thereafter. The citation curve of Hjort (1914) resembles this category of highly cited articles. Such a citation pattern implies that Hjort (1914) reports research–concepts–theories that are of continuing interest (e.g. by paradigm articulation or by developing particularly useful methods). We will take this up below.

Citations to 100-year-old publications are obviously very rare in the natural sciences. The large majority of citations are to recent publications. In 2004, the median age of cited literature in the natural sciences and engineering was about 7 years, while the mean was about 11 years (Lariviere *et al.*, 2008). The mean is significantly higher than the median because some older publications, such as Hjort (1914), are still cited. When interpreting the citation life cycle of Hjort's work, it must be noted that there has been a large increase in the overall volume of research in fisheries and marine biology. For example, the annual number of articles classified within the WoS category "Fisheries" increased from 1400 in 1981 to 4600 in 2011. We do not have corresponding statistics for the preceding period; however, the global production was surely lower at that time. Thus, the volume of articles that could cite Hjort (1914) is much larger today than in the past. However, this does not account for the rise in citations to Hjort (1914), since it has risen from ~5 per year before 1980 to 40–50 per year since

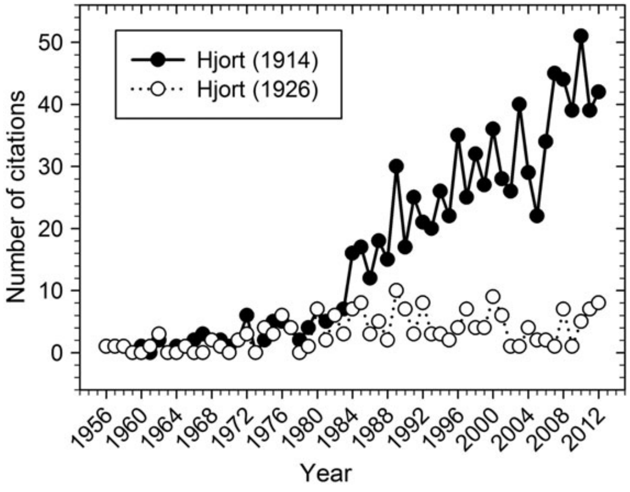

Figure 1. The absolute number of citations to Hjort (1914) and Hjort (1926) per year (1956–2012).

2006, an increase of 8–10 times while the overall growth in fisheries publications during the same period has been by a factor of 3.

During the first three decades of the time-series, Hjort (1914) and Hjort (1926) had similar citation rates (Figure 1). However, unlike Hjort (1914), the annual citation rate of Hjort (1926) did not rise significantly thereafter. Although we can only speculate, the differential citations to these two articles could be related to their somewhat different content and/or to the sociology of the citers (e.g. authors choose to cite the article that has been receiving more cites and, over time, that article becomes the only one that is cited and becomes the paradigmatic one).

In terms of the journals in which most citations to Hjort (1914) come from—not surprisingly, the list is strongly dominated by fishery and marine biology titles (Table 1); there are only a few citations from journals in other fields. The publication has been cited in 162 different journals, but the majority of these journals (104) have only cited the publication one or two times. *Marine Ecology Progress Series* (*MEPS*) is at the top of the list with 108 articles citing Hjort (from its foundation in 1979 to 2012). During this period, more than 12 000 articles have been published in *MEPS* and, therefore, almost 1% of the articles have cited Hjort (1914). After *MEPS*, follows the *Canadian Journal of Fisheries and Aquatic Sciences* (83 articles) and then the *ICES Journal of Marine Sciences* (52 articles).

Hjort (1914) has been cited by scientists in 53 countries—Hjort's work has had a broad and global impact on fisheries research. Approximately one-third of the authors citing Hjort (1914) are from the United States (Figure 2). Canada and Norway follow with 13 and 10% of the citations, respectively. The distribution of nationalities of citing authors corresponds loosely to the pattern of global scientific contributors within the fields of fishery and marine biology. For example, within the WoS category "Fisheries", the United States accounted for 23% of the global publication output during the period 1981–2011 (using the sum of all country's publication output as the denominator). The corresponding figures for Canada and Norway are 9 and 4%, respectively. Thus, researchers from the United States, Canada, and Norway tend to cite Hjort (1914) more often than those from other countries, relatively speaking. Hjort being a Norwegian scientist, this is not surprising for Norway and Hjort's connection to Canada and the fisheries on the east coast of North America was also strong (see Hubbard, 2014).

We used the wordle word cloud tool to visualize the most frequently appearing words in the tiles of articles that cite Hjort (1914; Figure 3). The size of a word in the word cloud is proportional to the number of times that it appears in the titles of the citing articles. The most frequently appearing words by far are *larval* and *larvae* with 178 and 171 appearances, respectively. Then follows *growth*, *fish*, and *recruitment* with frequencies in the range of 122–134 times. These word frequencies indicate that the topical themes of the citing articles are closely aligned with those taken up in Hjort (1914).

The citation context analysis, although limited to 37 highly cited articles, demonstrates clearly that Hjort (1914) is most often cited in the introduction of the articles. There are also many references to Hjort (1914) in the discussion of the articles. Typically, the introduction of a scientific article is structured as a progression from the general to the particular and often starts with references to the more general or basic works within a field. Consistent with this, references to Hjort (1914) are often found at the beginning of the text. Moreover, the citations are relatively uniform and the work

Table 1. List of the journals that cite Hjort (1914) most often (1956–2012).

Journal	# of articles	Journal	# of articles
Marine Ecology Progress Series	108	*Nippon Suisan Gakkaishi*	7
Canadian Journal of Fisheries and Aquatic Sciences	83	*Aquaculture*	7
ICES Journal of Marine Science	52	*Limnology and Oceanography*	7
Fisheries Oceanography	43	*Ecological Modelling*	7
Transactions of the American Fisheries Society	39	*Netherlands Journal of Sea Research*	7
Marine Biology	37	*Journal of the Marine Biological Association of the United Kingdom*	6
Fishery Bulletin	35	*Proceedings of the Royal Society B: Biological Sciences*	6
Journal of Fish Biology	32	*Nature*	6
Fisheries Research	19	*Fish and Fisheries*	6
Journal of Experimental Marine Biology and Ecology	18	*Plos One*	5
Journal of Sea Research	17	*California Cooperative Oceanic Fisheries Investigations Reports*	5
Bulletin of Marine Science	17	*Proceedings of the National Academy of Sciences of the United States of America*	5
Scientia Marina	14	*Marine and Freshwater Research*	5
Journal of Plankton Research	13	*Reviews in Fish Biology and Fisheries*	5
Ecology	13	*Advances in Marine Biology*	5
Environmental Biology of Fishes	12	*Fishery Bulletin of the National Oceanic and Atmospheric Administration*	4
Journal of the Fisheries Research Board of Canada	10	*Estuarine Coastal and Shelf Science*	4
Progress in Oceanography	9	*Biological Bulletin*	4
Journal of Marine Systems	9	*Archive of Fishery and Marine Research*	4
Deep-Sea Research Part II: Topical Studies in Oceanography	9	*American Naturalist*	4
Marine and Coastal Fisheries	8	*Trends in Ecology and Evolution*	4
Journal of Great Lakes Research	8	*Annual Review of Ecology and Systematics*	4
Ecological Applications	8	*North American Journal of Fisheries Management*	4
Fisheries Science	7	Other journals	167

tends to be cited for its hypotheses about advective loss, critical periods, and starvation (see Hare, 2014).

Garfield (1977) identified 15 reasons why a particular article might be cited. At least two of them seem particularly relevant for Hjort (1914): paying homage to pioneers and identifying original publications in which an idea or concept was discussed. The quotes below exemplify the first type of citation, which normally appear the article's introduction: "The importance of recruitment variability in the dynamics of exploited fish populations has been appreciated since the turn of the century (Hjort 1914)..." (Fogarty *et al*., 1991); "Pelagic fish stocks have been studied intensively, and, since the classic work of Hjort (1914), environmental factors are recognized as a determinant of recruitment success" (Cury *et al*., 2000). In these examples, Hjort (1914) is mentioned, although his theories do not necessarily play a central role in the article. The second, more specific type of referencing, "identifying original publications in which an idea or concept was discussed", also appears frequently for Hjort (1914). Such citations also usually occur in the introduction of the article. The following quotes illustrate this type of citation: "Documenting strong year classes in various fish stocks, Hjort (1914) was the first to articulate the idea that variation in larval survival may drive adult population dynamics" (Caley *et al*., 1996); "Hjort (1914) marked the beginning of a paradigm shift away from the migration theory to the view that fluctuations in adult abundance might be caused by variable recruitment..." (Swearer *et al*., 2002); "The match–mismatch theory first postulated by Hjort (1914) predicts that larvae hatching from eggs at a time when plankton densities are high will experience more rapid growth and higher survival than larvae produced when food is in short supply..." (Trippel, 1998). In addition to the two types of contextual referencing described above, other examples include articles where Hjort's work is cited in line with other literature as establish findings: "Variability has long been a recognised feature of the recruitments of marine organisms using broadcast reproduction (Hjort 1914, Coe 1953, 1956; Loosanoff, 1964, 1966, others in Underwood 1979)" (Doherty, 1983); "This is reflected by the dominance of single age cohorts for extended periods in both tropical and temperate species (e.g. Hjort 1914; Russ *et al*. 1996)" (Dulvy *et al*., 2003). The latter type of referencing is less frequent than the other two and occurs in both the introduction and discussion of articles. Overall, the contextual analysis demonstrates that Hjort (1914) is considered a seminal, novel, and paradigm setting study.

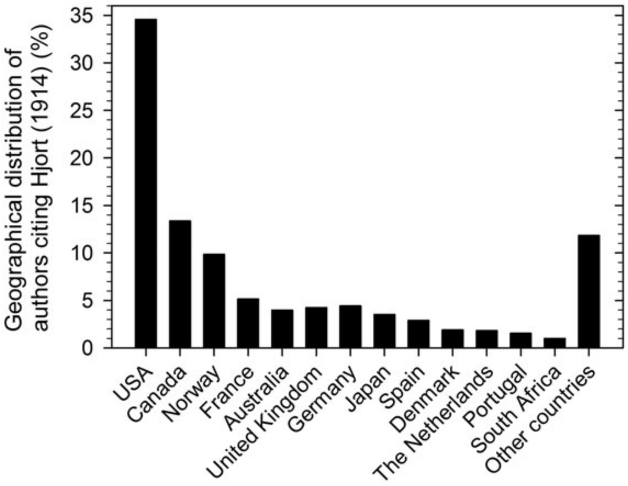

Figure 2. National distribution of authors citing Hjort (1914; 1956–2012). Note that articles with co-authors from more than one country are counted once for each country.

Generally, citations to older publications decrease as a result of the phenomenon termed "obliteration by incorporation": authors cease citing basic theoretical knowledge because it quickly becomes adopted as fact and/or the article unequivocally resolves the question that it took up. As a consequence, articles that present very basic and widely important findings may not be highly cited. One example of this is the article by Watson and Crick (1953) on

Figure 3. Illustration of the frequency of title words in articles citing Hjort (1914; 1956–2012). The size of the word is proportional to its frequency. Source: wordle.net.

the double helix structure of DNA, which is highly cited but not as frequently as one might expect for such a revolutionary contribution. Their findings were rapidly incorporated into the common body of accepted knowledge and, when this happened, researchers no longer cited it—everyone knew that the DNA molecule was a double helix. Importantly, for Hjort (1914), there is no evidence of this phenomenon; quite the contrary. We contend that this is because the core research questions addressed by Hjort (1914) remain unsolved and several of his hypotheses continue to drive fisheries science to this day (see Godø *et al*., 2014; Hare, 2014; Hutchings, 2014).

Acknowledgements

We are grateful to Caroline Durif for help drafting the figures and for comments on an earlier draft.

HIB's contribution to this article was supported by Projects # 81529 ("Fine scale interactions in the plankton") and 83741 ("Scientific publishing and editing") from the Institute of Marine Research, Norway.

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ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2017–2025. doi:10.1093/icesjms/fsu076

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Where we are

Original Article

Autumn bloom phenology and magnitude influence haddock recruitment on Georges Bank

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Leaf, R. T., and Friedland, K. D. Autumn bloom phenology and magnitude influence haddock recruitment on Georges Bank. – ICES Journal of Marine Science, 71: 2017–2025.

Received 2 July 2013; revised 1 April 2014; accepted 4 April 2014; advance access publication 3 June 2014.

The haddock (*Melanogrammus aeglefinus*) stock on Georges Bank in the Northwest Atlantic is characterized by extremely large recruitment events relative to spawning-stock biomass. Recent work has indicated that the dynamics of the preceding autumn bloom may have explanatory power to describe these events. In this paper, we examine the hypothesis that autumn phytoplankton dynamics affect the recruitment of haddock, examine the temporal and spatial characteristics of the autumn phytoplankton bloom on Georges Bank, and correlate individual sex-specific condition measurements of haddock made in spring to recruitment patterns. Autumn bloom characteristics vary considerably across Georges Bank with earlier-occurring and larger-integral blooms occurring on the northern flank. On average, autumn blooms start on day 273 (29 September) and persist ~50 days. There was a significant negative correlation detected between bloom start date and recruitment and a significant positive correlation of bloom integral and recruitment. The survivor ratio $\log_e(R/SSB)$ was positively and significantly correlated with individual condition of females in spring. The analysis of autumn bloom on Georges Bank provides a predictive index for recruitment strength of haddock and has utility for the assessment of this stock.

Keywords: bloom timing, haddock, parental effects, phenology, recruitment.

Introduction

Understanding the mechanisms responsible for the variation in year-class strength of harvested marine populations continues to be one of the primary challenges to fisheries oceanographers, as it was to Hjort in the early days of the science (Hjort, 1914; Houde, 1987; Cushing and Horwood, 1994). A comprehensive understanding of the causes of recruitment variation remains elusive, although it is a "characteristic feature" (Hjort, 1914) of many stocks. Similarly, the ability to make quantitative predictions of year-class strength is difficult because a variety of abiotic and biotic forcing mechanisms interact (Begg and Marteinsdottir, 2002; Govoni, 2005; Pitchford *et al.*, 2005; Payne *et al.*, 2009a). These factors influence stock productivity at all phases of ontogeny, providing a wealth of potential junctures or "bottlenecks" in the reproductive cycle where recruitment may be determined (Houde, 2008). It has been a challenge to identify where these recruitment bottlenecks occur, both because many recruitment factors are seemingly disparate and can co-vary with other biological and physical forcing variables (Myers, 1998; Miller *et al.*, 2011). One approach to increasing the performance in the prediction of year-class strength is the identification of tractable short- and long-term ecosystem drivers that co-vary with the observed fluctuations of the stock (Fritz *et al.*, 1990). Such an approach is appropriate given the long-term empirically derived and modelled time-series of both oceanographic conditions and fish abundance that now exists for some areas and fish stocks (Greenstreet and Hall, 1996; Klyashtorin, 1998; Fogarty *et al.*, 2001; Hare and Able, 2007).

Georges Bank, which is part of the US Northeast continental shelf ecosystem, is a well-studied area with respect to its resident fish populations and oceanographic conditions. The ecosystem is highly productive and supports commercial fisheries on a number of finfish and shellfish species. Of the groundfish species, Georges Bank haddock (*Melanogrammus aeglefinus*) is a valued fisheries target, which exhibits marked variation in annual year-class strength (Overholtz *et al.*, 1986; Fogarty *et al.*, 2001). The recruitment dynamics of Georges Bank haddock are characterized by punctuated events of extremely large year-classes, which are critical for sustaining harvestable biomass. Although haddock recruitment is positively correlated with stock size, there is considerable variation in this relationship (Brodziak *et al.*, 2001). The source of variation in Georges Bank haddock recruitment has been the subject of considerable debate, the importance of which has been underscored by the occurrence of yet another large year class in 2010 (Northeast Fisheries Science Center, 2012).

Haddock possess a complex life history and a number of potential recruitment bottlenecks has been identified and investigated. Recruitment strength of haddock has been associated with spring bloom productivity and its role in the survival of larval haddock (Platt *et al.*, 2003; Munk, 2007; Buckley *et al.*, 2010). These studies have addressed both spatial and temporal aspects of the spring bloom and the benefits that high levels of primary productivity have to increase larval feeding opportunities. Mountain and Kane (2009) have found an association of larval survivorship of haddock and zooplankton community structure, suggesting that shifts in size spectra of zooplankton may affect haddock recruitment success. That larval retention may be important to recruitment and determined by water circulation patterns on Georges Bank has been suggested as well (Smith and Morse, 1985; Myers and Drinkwater, 1989). It is clear that spawning haddock on Georges Bank are concentrated in an area that favours larval retention and presumably enhances their access to prey and preferred settlement habitats (Page *et al.*, 1999; Lough *et al.*, 2006; Lough and O'Brien, 2012). The timing of haddock spawning has also been investigated, suggesting that earlier hatched haddock have a greater likelihood of surviving to become juvenile recruits (Head *et al.*, 2005; Lapolla and Buckley, 2005). Episodic recruitment events have also been associated with the autumn bloom on Georges Bank the year before spawning, suggesting that parental condition is important to the observed contrast in recruitment (Friedland *et al.*, 2008). It is this later hypothesis we examine further, in the light of the additional recruitment events that have occurred since it was first suggested and mindful of the fact that the former hypotheses of recruitment control are with foundation. We believe all these factors work in concert to control Georges Bank haddock recruitment. The outstanding issue is which of these has the best predictive power to describe the recruitment dynamics of this population.

The parental condition hypothesis suggests that year-class strength in haddock is determined by prespawner provisioning (Friedland *et al.*, 2008). Blooms of large magnitude, the intensity of which is defined as the integral, result in a flux of energy to the benthos. Since juvenile and adult haddock consume primary detritivores (Wigley and Theroux, 1965), large dimension blooms will provide energy to this prey source. We hypothesize that the trophic response of haddock to this input of energy is to shunt more energy into somatic growth and gonad formation during the months before spawning. The result being an increase in condition, the production of more gametes (Rickman *et al.*, 2000) or the production of gametes of greater quality (Marteinsdottir and Steinarsson, 1998; Donelson *et al.*, 2008), or a combination. In this study, we evaluate the effects of autumn bloom phenology and spatial dynamics on haddock recruitment. We accomplish this by spatially stratifying the Georges Bank ecosystem, guided by a qualitative analysis of bloom patterns and on a regular grid. We describe the temporal productivity dynamics on Georges Bank and relate estimated bloom parameters to recruitment. Finally, we examine how recruitment correlates to indices of sex-specific individual condition, measured in spring.

Material and methods

To describe how the phenology and spatial extent of the autumn phytoplankton bloom on Georges Bank influences haddock recruitment, we first evaluated the relationship of recruitment and stock size for the entire time-series of these data (1960–2010). Two models, Cushing (1971) and Ricker (1954), were used to describe the relationship between stock size (S, 10 000 mt) and recruitment (number of age-1 recruits). The Cushing model is $f(S) = \alpha S^{\gamma}$, and the parameters are α, which controls the steepness of the curve, and γ which controls the shape of the curve (the relationship is linear for $\gamma = 1$). The dome-shaped Ricker (1954) model is defined as $f(S) = \alpha S e^{-\beta S}$, and the model parameter α is the slope of the function near stock size of zero and the spawning-stock size at maximum recruitment is $1/\beta$.

Year-specific survivor ratio for haddock for the period for which environmental (ocean colour) data were available was calculated as the age-1 abundance (number of individuals) divided by the spawning-stock biomass of the previous year (SSB mt, Northeast Fisheries Science Center, 2008, 2012). These data included recruitment years 1998–2010 and were obtained from age-structured population assessment. Following Friedland *et al.* (2009), the recruitment data were $\log_e$ transformed.

Chlorophyll *a* measurements were made on Georges Bank 1997–2009 using ocean-colour images taken by the Sea-viewing Wide Field of View (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) sensors. The spatial extent of the analysis was limited to the Georges Bank region and was evaluated at various spatial scales (Figure 1). Data from these two sensors provide an overlapping and nearly uninterrupted time-series of ocean colour images from 1997 to present. We used level-3 processed

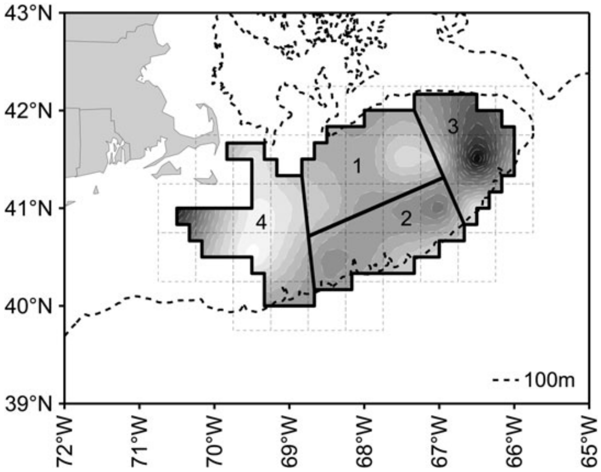

Figure 1. Map of the Georges Bank area of the US Northeast continental shelf. The highlighted area is the Georges Bank ecoregion, which is subdivided into four subregions (1–4) qualitatively identified by examining the first principal component of the monthly chlorophyll *a* concentration, shown as contours within the ecoregion. Dashed lines mark a regular 0.5° sample grid that overlaps the ecoregion. The dotted line is the 100 m isobath.

data, at 9 km and 8-d spatial and temporal resolution, respectively, from the Ocean Color website (oceancolor.gsfc.nasa.gov).

We examined autumn bloom patterns at three levels of spatial resolution: (i) the Georges Bank ecoregion; (ii) a set of four subregions of the ecoregion determined by temporal patterns in the chlorophyll concentration; and (iii) a regular spatial grid of 0.5° resolution (Figure 1). The ecoregion-level analysis reflects the division of the regional shelf sea into production units (Ecosystem Assessment Program, 2012). We divided the ecoregion into subregions based on monthly aggregated composite images of chlorophyll *a* concentration and identified areas that shared similar autumn bloom characteristics. Principal component analysis (PCA) was performed on these data and the first principal components of each time-series were plotted. We used kriging interpolation and identified regions on Georges Bank with similar values in the integral of their first principal components. These were qualitatively aggregated as unique subregions within the larger Georges Bank ecoregion. The 0.5° square grid included all grid locations that overlapped the ecoregion.

The chlorophyll *a* value at each 8-d period, for all levels of resolution, was calculated by taking the average of the constituent pixel elements. Regardless of the spatial resolution, we used linear interpolation to fill in any single missing values within the extent of the data and filled missing values at the beginning and end of the time-series with first and last observations, respectively, thus completing each chlorophyll *a* time-series. Because we were interested in the autumn bloom dynamics, we limited the analysis to the second half of the year and used the 23 8-d chlorophyll periods starting on day 185 and ending on day 361 (beginning of July to the end of December).

Characterization of autumn bloom dynamics was determined using a sequential averaging algorithm called STARS or "sequential *t*-test analysis of regime shifts" (Rodionov, 2004, 2006). The method has been used in previous analyses of Georges Bank autumn blooms (Friedland *et al.*, 2008, 2009) and elsewhere (Friedland and Todd, 2012). The STARS algorithm is a filtering method that involves processing the time-series under investigation to identify statistically significant structural changes in the mean. The STARS algorithm requires that three parameters be specified. The first is the α-level for a change in the mean to be considered significant and this was set to $\alpha = 0.05$. The second parameter is the length criteria, the number of time-steps (the duration of a time-step in this analysis is 8 d) to use when calculating the mean level of a new regime, this was set to 5. Finally, the Huber weight parameter was set to 3; this parameter determines the relative weighting of outliers in the calculation of the regime mean. We considered a bloom to have occurred if there was an 8-d period bracketed by a positive and negative structural change and a structural change (positive or negative) could not occur in the first or last two 8-d periods to be scored. Finally, a recognized bloom could not exceed nine sample 8-d periods (~2.4 months). This scoring rule was based on preliminary analysis of Georges Bank autumn blooms. We found that the median bloom duration was six 8-d periods and the inter-quartile range of bloom duration was five to eight 8-d periods. Bloom lengths exceeding or equal to nine 8-d periods were determined to be basically different in their structure to the typical, discrete blooms observed during the autumn. We considered these longer, seasonal changes in chlorophyll concentration to have different ecological implications to the benthos, specifically, the reduced ability to export energy.

For each detected bloom, we extracted statistics to characterize bloom timing and dimension. Bloom start was defined as the day of initiation of the autumn bloom: The first day of the 8-d period that exhibited bloom conditions. Bloom average is the average chlorophyll concentration during the bloom period and bloom integral was the integral of the chlorophyll concentrations for the bloom period. In some years and locations, no distinct autumn bloom period was detected by the STARS algorithm. When no bloom was detected, the bloom average and integral were based on chlorophyll concentrations from a climatological bloom period and bloom start was treated as a missing value. The climatological bloom period was based on the mean start and end dates of observed blooms. The Pearson product–moment correlation was used to test the direction and magnitude of the correlation of survivor ratio to bloom start, average and integral.

As a further characterization of the effect of bloom dynamics on haddock, we evaluated the relationship of recruitment and condition. We determined the Pearson product–moment correlation of survivor ratio, $\log_e(R/\mathrm{SSB})$, and mean sex-specific condition of Georges Bank haddock collected in spring (April) to determine

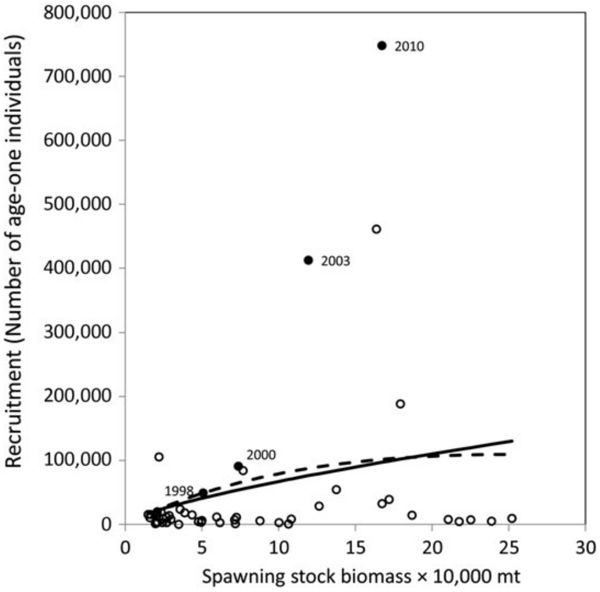

Figure 2. Relationship of SSB (×10 000 mt) and recruitment (number of age-1 individuals) for the Georges Bank haddock stock with Cushing (solid line) and Ricker (dashed line) stock recruitment curves. Extraordinary year classes 1998, 2000, 2003, and 2010 (closed circles) are identified.

Table 1. Summary of estimated SSB, recruitment strength (*R*) defined as the number of age-1 individuals for the following year, survivor ratio (*R*/SSB), and log of the survivor ratio.

Year	SSB, mt	*R*, 10^3	R/SSB	log R/SSB
1998	50 807	49 156	0.968	−0.014
1999	59 528	11 668	0.196	−0.708
2000	73 600	90 866	1.235	0.092
2001	87 872	5 551	0.063	−1.199
2002	100 258	2 870	0.029	−1.543
2003	119 310	412 375	3.456	0.539
2004	108 126	7 985	0.074	−1.132
2005	126 290	28 833	0.228	−0.641
2006	225 173	7 123	0.032	−1.500
2007	252 065	9 365	0.037	−1.430
2008	238 744	4 773	0.020	−1.699
2009	210 557	7 605	0.036	−1.442
2010	167 279	748 016	4.472	0.650

if a positive relationship existed. Condition is a morphological weight–length index of nutritional and health status of an individual (Richter *et al.*, 2000). Individual condition was calculated using Fulton's condition factor, $K = 10\,000 \times W/L^3$, where W is the weight of an individual haddock (kg) and L the fork length of an individual (mm) collected in spring (April) from 1992 to 2010 on Georges Bank (Froese, 2006). The number of haddock analysed for each year, for each sex, ranged from 41 to 449 individuals (the

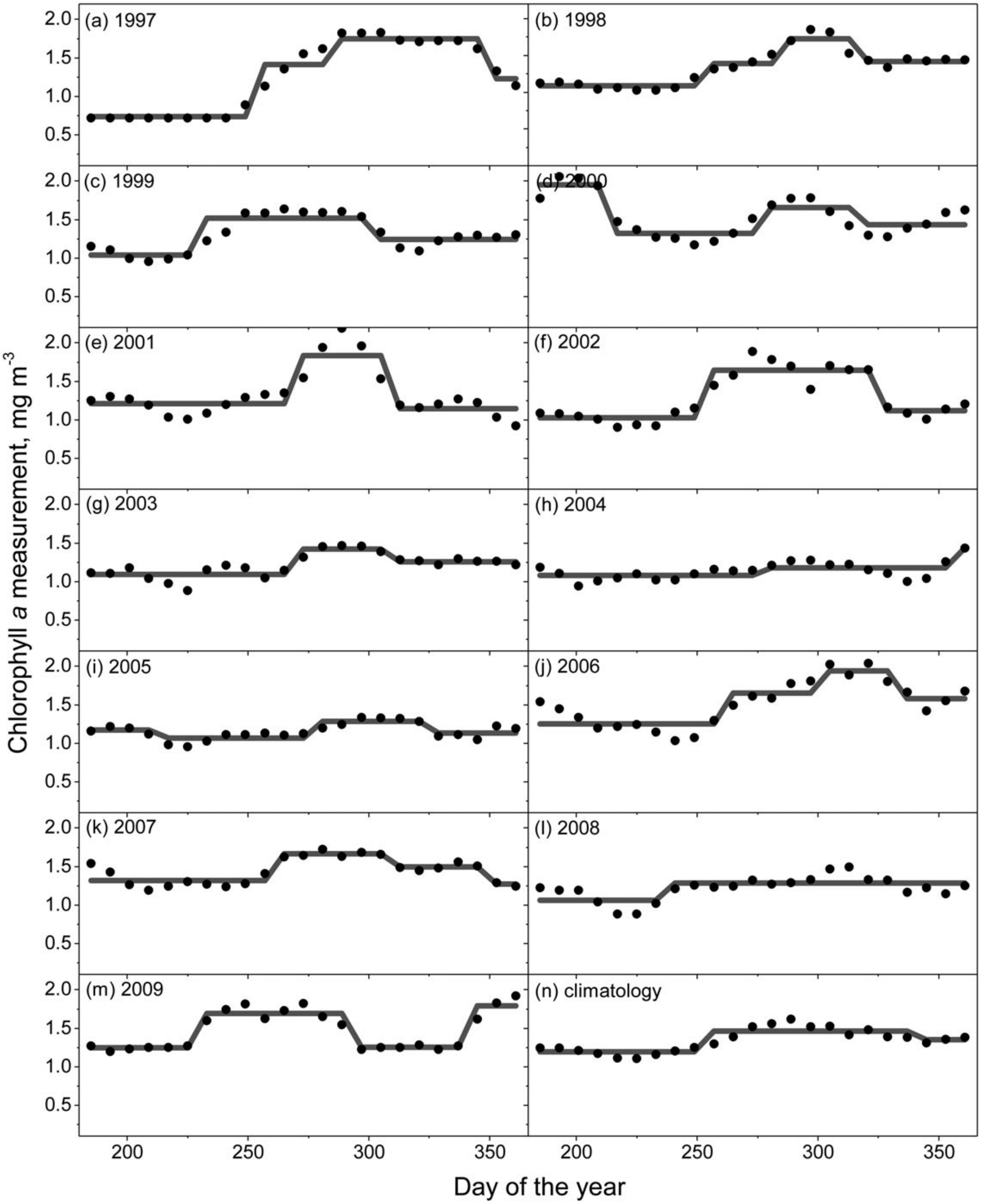

Figure 3. Time-series of three-period moving average smoothed of 8-d chlorophyll *a* measurements (mg m^{-3}, points) and STARS algorithm fit to time-series (solid line) for the years 1997–2009 (a to m, respectively) and for data climatology (n) over autumn season (days 176–361).

Table 2. Table of the average autumn bloom dynamics for the entire Georges Bank region and for each of the designated subareas established in this study.

	Observed blooms				Climatological bloom		All years	
Local	**Start**	**End**	**Number**	**Duration**	**Start**	**End**	**Integral**	**Average**
Georges Bank	272.3	312.3	11	6.0	273	313	9.58	1.62
Area 1	257.0	301.0	6	6.5	257	297	13.38	2.17
Area 2	274.1	314.1	7	6.0	273	313	7.45	1.29
Area 3	255.9	297.0	7	6.1	257	297	8.18	1.35
Area 4	277.6	319.9	7	6.3	281	321	9.28	1.51

The mean autumn bloom start day, end day, and duration is the average of the available years (Number) from (1997 to 2012) for which a autumn bloom was detected. The climatological period is the nearest 8-d start and end day to the observed bloom period. The integral and average for all years is the mean mg m^{-3} chlorophyll *a* for all autumn blooms.

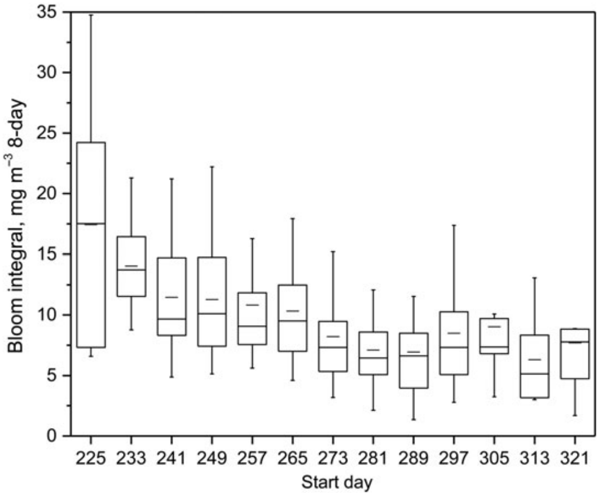

Figure 4. Boxplots of bloom integral (mg m^{-3}) binned by bloom start date for blooms detected in 0.5° grid locations for all years over Georges Bank.

Table 3. Correlation table of the $\log_{10}$ of the number of age-1 recruits ($\times 10^3$) per SSB (mt) and the integral (mg m^{-3}) and average (mg m^{-3} d^{-1}) of chlorophyll *a* and the start date of autumn blooms in the entire Georges Bank region and for each of the designated subareas established in this study from 1998 to 2009.

	Magnitude		Average		Start date		
Local	***R***	***p*-value**	***R***	***p*-value**	***R***	***p*-value**	***n***
Georges Bank	**0.80**	**0.00**	0.07	0.81	**−0.61**	**0.05**	11
Area 1	**0.70**	**0.01**	0.30	0.31	−0.76	0.14	5
Area 2	0.21	0.49	0.23	0.45	−0.25	0.60	7
Area 3	0.47	0.11	0.22	0.46	−0.61	0.15	7
Area 4	0.00	0.99	−0.11	0.73	0.86	0.06	5

The *p*-value is the probability value of the regression. *R* is the Pearson product–moment correlation coefficient. Values in bold font indicate that the *p*-value of the correlation is less than 0.05.

median number of individuals in the determination of the annual sex-specific condition is 163.5). Fish were collected during NOAA's Northeast Fishery Science Center fishery-independent annual spring groundfish survey.

Results

The first principal component of the monthly chlorophyll *a* time-series, evaluated on Georges Bank at 0.5 × 0.5° resolution, indicates that there is heterogeneity in chlorophyll concentration patterns within the region (Figure 1). Our spatial unit of analysis is indicated by the boundaries of the polygon in Figure 1, and these boundaries are generally coincident with the Georges Bank haddock stock management boundaries and the bathymetry of the Bank. We identify four areas on Georges Bank with distinct properties in the PCA analysis of monthly aggregated chlorophyll *a* dynamics.

Haddock recruitment has varied greatly in relation to SSB from 1960 to 2010 (Figure 2). The patterns of estimated SSB and recruitment revealed four large year classes that occurred between 1998 and 2010 (Figure 2, Table 1) including the first and last years of the period and the years 2000 and 2003. The fit of the Cushing model to the entire time-series, 1960 to 2010, indicated a generally positive relationship of SSB and recruitment (Figure 2), but this relationship was not statistically significant ($p > 0.05$). There is very little difference in the expected mean magnitude of recruitment and SSB among the two model forms analysed (Cushing and Ricker) and both of these model fit the data poorly (Cushing $R^2 = 0.07$ and Ricker $R^2 = 0.06$).

The STARS estimates of autumn chlorophyll *a* patterns of Georges Bank resulted in simplified patterns of the 8-d point estimates, from which the average, integral, and phenology could be determined (Figure 3). Variation in the timing of initiation of autumn bloom conditions was evident and ranged from days 233 to 305 (20 August to 31 October). The mean start day was 271 (27 September) and the bloom was terminated, on average, at day 313 (8 November). Autumn bloom phenology in 1999 and 2009 were the earliest recorded, occurring at day 233 (20 August). Autumn bloom initiation for 2002 was the second earliest, occurring at day 257 (13 September). The 3 years for which early start dates of autumn bloom were identified also had the longest bloom duration of seven to eight 8-d periods. Autumn bloom in 1997 lasted seven 8-d periods and was the only year which had estimated bloom duration longer than five 8-d periods. There were also absences in the detection of autumn bloom in 2004 or 2008 (Figure 3h and l). The mean value of chlorophyll *a* in the time-series was 1.62 mg/m^2 chlorophyll *a* across the entire Georges Bank region (Table 2). The largest mean peak chlorophyll a values occurred in 1997, 2001, and 2006 with integrals ranging from 1.74 to 1.94 mg/m^2 chlorophyll *a*. The mean value of chlorophyll *a* from autumn blooms in years 1999, 2002, and 2009 was similar to that of chlorophyll *a* for all autumn blooms examined, ranging from 1.52 to 1.69 mg/m^2 chlorophyll *a*. The integrated chlorophyll *a* for the identified bloom period was greatest for autumn blooms in 1997, 1999, 2002, and 2009, ranging from 13.50 to 14.77 mg/m^2 chlorophyll *a*. These were the only blooms that had integrals exceeding 10.0 mg/m^2 chlorophyll *a*.

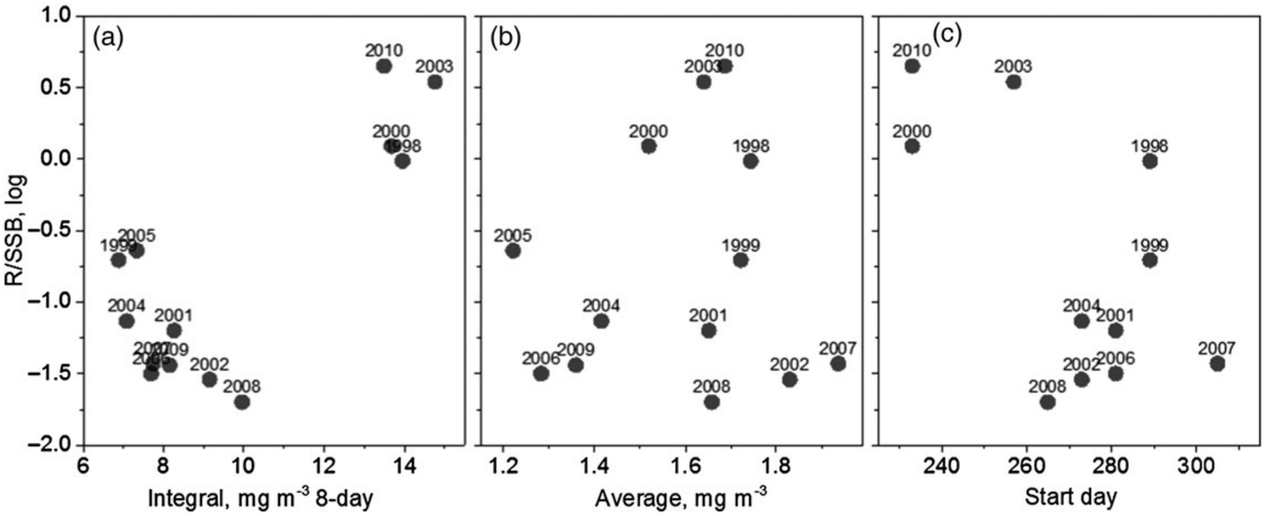

Figure 5. Scatterplot of haddock survivor ratio and integral (a), average (b), and start date (c) of autumn blooms detected in the Georges Bank ecoregion.

Spatial differences exist in the phenology and magnitude of the chlorophyll *a* bloom dynamics of the four regions identified on Georges Bank (Table 2, Figure 3). Areas 1 and 3 are characterized by early bloom initiation relative to the other subregions and the whole of Georges Bank. Area 1 is unique in the large bloom average it exhibits, which results in an elevated chlorophyll *a* integral relative to the other subregions. Our ability to detect autumn blooms in each of the subregions was reduced ($n = 6–7$), relative to the detection of the entire region ($n = 11$). We detected a weak negative relationship of autumn bloom integral and day start (Figure 4).

The subregion and whole Georges Bank patterns in phenology and integral of observed autumn blooms are correlated with the observed recruitment time-series (Table 3). The integral and phenology of autumn bloom on Georges Bank is strongly and positively correlated with the annual recruitment index $R \times 10^3/\mathrm{SSB} \times 10^4$ (Figure 5). Only Area 1 of Georges Bank has a significant correlation to the recruitment index (Table 3): the integral of autumn bloom in this area is positively correlated with recruitment.

Gridded, kriged spatial analysis indicates that Area 1 is a centre of autumn bloom phenology and the characteristic dynamics that are correlated with recruitment success (Figure 6). Area 1 exhibits earlier dates of autumn bloom initiation and greater bloom average and integrals than other areas. Autumn bloom start dates increase (occur later) to the south and west on Georges Bank. Similarly, regions to the south and west of area 1 have a decrease in average and integral across most of the region except the area located farthest west.

We found a correlation between the mean annual condition of haddock on Georges Bank collected in April and survivor ratio of the year class using the Pearson product–moment correlation. The positive relationship was weak for both males ($r = 0.424$) and females ($r = 0.517$), but the relationship of female mean Fulton's condition factor and the survivor ratio was statistically significant ($p = 0.023$). The notable year classes in 1998, 2000, 2003, and 2010 are not consistently associated with greater magnitudes of Fulton's *K* measured in spring (Figure 7). The mean female condition for 2010 was the fourth lowest measured value (Fulton's $K = 0.93$). The mean female condition for 1998, 2000, and 2003 were not consistently the greatest magnitude *K* values, ranking fifth, third, and tenth greatest, respectively, of the condition estimates ($n = 19$).

Discussion

Autumn phytoplankton blooms on Georges Bank are conspicuous features during some years and, like the observed pattern of haddock recruitment, are marked by interannual variability. The primary finding in this work is that autumn blooms occurring on the northern edge of Georges Bank are especially important to the recruitment dynamics of haddock and that recruitment is facilitated by blooms that occur early in autumn season and are of large magnitude. The proposed mechanism of trophic transfer to females is supported by the observed positive and significant correlation of recruitment and individual condition of females. Autumn blooms have been shown to be important to haddock recruitment success on Georges Bank and we provide a mechanism of this process, maternal provisioning, by analysing the spatial and temporal dimensions of autumn bloom, condition dynamics, and recruitment patterns.

Our assessment that some metrics of autumn bloom are important to haddock year-class strength has a spatial component. Large integral blooms, which are positivity correlated with year-class strength, are centred on the north-central and northern flank areas of Georges Bank. Bloom conditions in this area supply particulate organic carbon to the northeast peak region via clockwise gyre circulation observed on the Bank (Butman *et al.*, 1982). The northeast peak of Georges Bank has been recognized as an area of aggregation for prespawning haddock (Lough *et al.*, 2006; Lough and O'Brien, 2012). Early bloom conditions should allow more time for transport of surface production to benthic foodwebs (Townsend and Cammen, 1988) and long-lasting blooms may provide the most energy to benthic primary and secondary consumers which are a major prey item of haddock (Wigley and Theroux, 1965). The identification of subregions of Georges Bank, where productivity and oceanographic characteristics act at different stages of ontogeny to maximize recruitment of haddock, is a necessary step to understanding the environmental dynamics that influence population productivity.

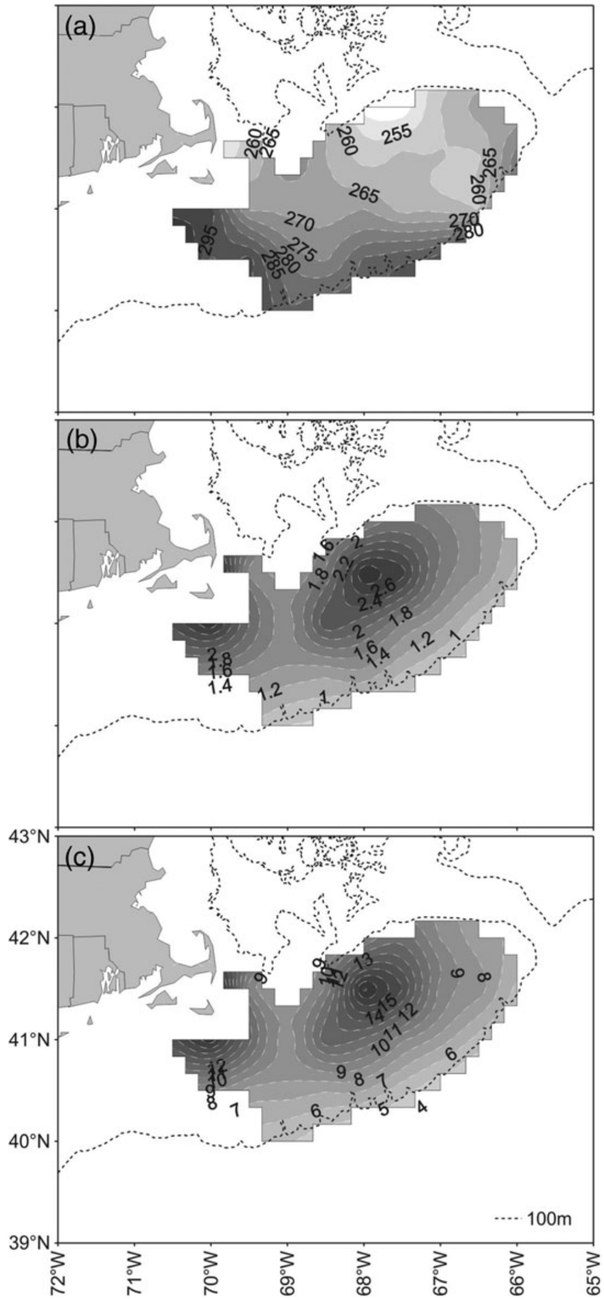

Figure 6. Contour maps of autumn bloom mean start day of the year (a), mean bloom average (b), and mean bloom integral (c) based on 0.5° grid data over the Georges Bank ecoregion for the period 1997–2011. Units: average (mg m^{-3}) and integral (mg m^{-3} 8-d).

Payne *et al.* (2009b) stated that the efficacy of the maternal provisioning hypothesis is contingent on a series of conditional steps, each subject to considerable environmental variability. The difficulty in the prediction and the challenges to the understanding of recruitment patterns implies that such complexity is likely a common factor for most fish recruitment dynamics (Myers, 1998). Our conceptual model of haddock recruitment, where maternal condition may be paramount to recruitment success, is that bottlenecks occur throughout the life history of an organism and that such bottlenecks begin at the egg stage.

Maternal somatic and reproductive condition in some fish species has been shown to be influenced by environmental conditions (Ventresca *et al.*, 1995) and improvement in maternal condition has been shown to increase egg size and egg quality. These characteristics relate to larval viability (Donelson *et al.*, 2008). For example, Marteinsdottir and Steinarsson (1998) reported that Atlantic cod (*Gadus morhua*) larval size at hatching increased with egg size, and that measures of larval viability, including feeding success, swimbladder development, and growth rates at age 15 days, were positively correlated with egg size and weight. Probst *et al.* (2006) examined parental effects on the life history traits of haddock. They found that maternal influences on larval standard length and yolk area were significant. Maternal provisioning may provide the proximal cause of larval survival because larger larvae are better at evading predators due to greater swimming speeds (Batty *et al.*, 1993) and have increased sensory development (Fuiman, 1989). Our assessment that the survivor ratio is positively correlated with female condition is indicative that the trophic mechanism of increased productivity in autumn provisions spawning females, leading to increases in individual condition and reproductive output.

Large autumn blooms on Georges Bank are a cause for and a consequence of large-scale biological and oceanographic dynamics. Autumn phytoplankton blooms, like those in spring, are driven by oceanographic processes at large spatial and temporal scales (Song *et al.*, 2010). The connectivity of bloom conditions to these dynamics implies that there may be alternative mechanisms to maternal provisioning and that these may be responsible for the observed strong haddock year-classes following an early and large-integral autumn bloom. One potential alternative hypothesis is that strong autumn bloom conditions promote survival of overwintering of the copepod *Calanus finmarchicus* (Meise-Munns *et al.* 1990), the eggs of which are major prey species of haddock larvae (Kane, 1984). Another alternative is that the large-scale oceanographic factors that promote productive autumn bloom conditions are responsible for spring conditions that promote retention of larvae on Georges Bank. Page *et al.* (1999) and Lough *et al.* (2006) have reported the importance of cod and haddock larvae being retained on Georges Bank during spring such that they will settle in optimal habitats.

Before the strong year class in 2000, the haddock stock in Georges Bank was characterized by low SSB and generally poor year classes relative to stock size (Overholtz *et al.*, 1986). Episodic recruitment events, such as those most recently observed in 2010, are critical for fishery sustainability and the two strong year classes observed in 2000 and 2003 provided the biomass to build the stock to its current level, above the SSB at MSY (Northeast Fisheries Science Center, 2008, 2012). We find that the integral and timing of autumn phytoplankton bloom on Georges Bank is significantly correlated with haddock recruitment. The potential effects of maternal provisioning have not been widely studied for wild fish stocks and we suggest that such a mechanism may be important to the recruitment dynamics of other spring-spawning fish.

The results of this work indicate that autumn bloom timing and integral is a potentially powerful predictive tool for forecasting haddock recruitment. Our results further support the hypothesis that maternal provisioning is the mechanism that leads, in part, to strong year classes of haddock on Georges Bank. This conclusion is consistent with an expanded interpretation of Cushing's (1990) match–mismatch hypothesis: that fitness is maximized when predator requirements maximally overlap, in time and space, prey

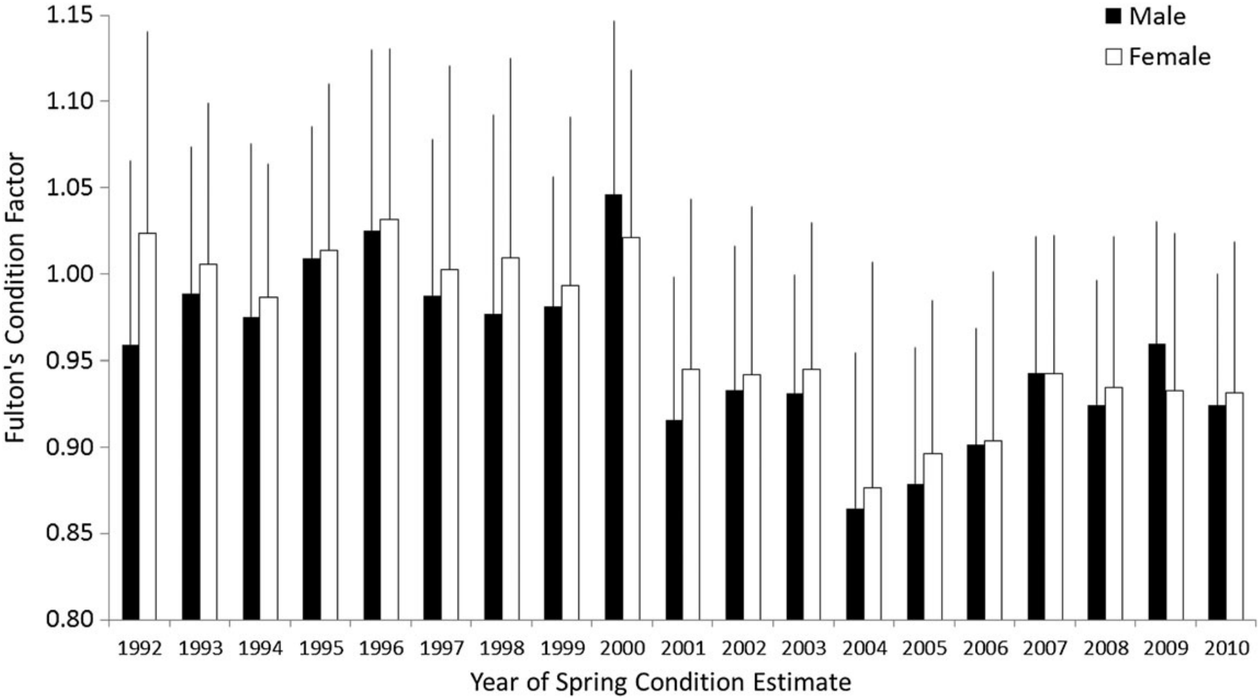

Figure 7. Mean male and female Fulton's condition factor (error bars are 1 s.d.) for spring (April) from 1992 to 2010. The calculation of the mean and standard deviation of each annual sex-specific condition factor was based on $n = 43-420$ measurements for males and $n = 41-441$ measurements for females.

availability during some critical life stage (Durant *et al.*, 2007). Historically, this critical life-stage has been recognized as the larval stage; however, we show that a potential bottleneck for the Georges Bank Haddock may occur earlier in ontogeny.

Acknowledgements

This work was supported by funding from the National Marine Fisheries Service Fisheries and the Environment (FATE) program. We particularly thank M.J. Fogarty for his thoughtful review of an early draft of the manuscript.

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Handling editor: Manuel Hidalgo

ICES Journal of
Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2026–2041. doi:10.1093/icesjms/fsu070

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

North Sea herring (*Clupea harengus* L.) recruitment failure may be indicative of poor feeding success

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Lusseau, S. M., Gallego, A., Rasmussen, J., Hatfield, E. M. C., and Heath, M. North Sea herring (*Clupea harengus* L.) recruitment failure may be indicative of poor feeding success. – ICES Journal of Marine Science, 71: 2026–2041.

Received 30 June 2013; accepted 28 March 2014; advance access publication 12 May 2014.

Recruitment of the 2002–2012 year classes to the North Sea herring stock has been below expectations given the spawning biomass, due to exceptionally low overwinter survival of larvae. Here, we investigate whether changes in survival of larvae in the northwestern North Sea could be attributed to changes in parasite prevalence or feeding conditions. We used a method that combined particle tracking models and survey data to estimate survival, and microscopic examination of gut contents of archived samples of larvae collected in February each year between 1995 and 2007 to investigate parasite prevalence and feeding. We deduced that we can use the incidence of tetraphyllidean parasites as an index of the cumulative feeding history of the larval population. We found that the prevalence of larvae of a tetraphyllidean cestode in the gut contents varied significantly between years and was positively correlated with feeding success. High feeding success, indicated by high prevalence of tetraphyllideans, influenced survival by offsetting the effect of a second parasite type, a digenean trematode. We suggest that variability in cumulative food intake over the lifespan up to February is a significant determinant of variability in survival.

Keywords: feeding success, fish larvae, North Sea herring, overwintering, parasites, recruitment, survival.

Introduction

The North Sea herring stock has experienced a sustained and unprecedented period of low productivity since 2002 (Payne *et al.*, 2009). Although the spawning-stock biomass has been consistently high and well above the level where impaired recruitment is expected to set in, the number of recruits produced per spawner continues to be at the lowest levels recorded (ICES, 2013).

In the northwestern North Sea, herring spawn along the east coast of Scotland and around the Orkney and Shetland Islands, with spawning commencing in the north around August–September and progressing south into the early winter (Heath and Richardson, 1989). The larvae develop over winter and metamorphose in early spring the following year. During this period, the developing larvae are fully planktonic and disperse with the prevailing currents to a potential North Sea-wide distribution. It is over this period that the strength of the recruiting year-class in North Sea herring is determined (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009).

The International Council for the Exploration of the Seas (ICES) coordinates two surveys of North Sea herring larvae. The first one is carried out in autumn and produces an index of abundance of newly hatched larvae on the spawning grounds. The second survey is carried out towards the end of winter and measures abundance of the late stage larvae that have survived winter development period. Despite a consistently high larval production measured in autumn surveys, the abundance of late stage larvae just before metamorphosis is at an all-time low (ICES, 2013). The poor recruitment, it is concluded, is linked to increased mortality rates during this overwinter larval development period (Payne *et al.*, 2009; Fässler *et al.*, 2011). The causes of the increased mortality remain under investigation and several explanatory hypotheses have been proposed (ICES, 2007).

Corten (2013) argued that cannibalism by adult herring could explain the change in survival. Hufnagl and Peck (2011) used a physiological individual-based model of the foraging and growth of herring larvae to demonstrate a possible link with temperature and prey composition and concentrations, with the timing around first feeding being particularly sensitive. Increased temperatures, particularly in the northern North Sea, were also linked to increased mortality rates in the northern components of herring larvae by

Fässler *et al.* (2011). Payne *et al.* (2009) and ICES (2007) suggested a link between the poor herring larvae survival and changes in the North Sea physical and biological environment. Edwards *et al.* (2007) documented a shift in the North Sea plankton community towards a more diverse warmer-water community around 2000, just before the onset of the period of poor herring recruitment (Payne *et al.*, 2009). A similar regime shift in the North Sea in the late 1980s has been linked to reduced survival of larvae of Atlantic cod (*Gadus morhua* L.) in the North Sea through changes in the availability and suitability of prey (Beaugrand *et al.*, 2003). The increased temperature in the North Sea has also been linked to changes in the distribution of many fish species, with the potential for increased predation on herring larvae (Payne *et al.*, 2009). Coincidences between changes in herring larvae survival and, for example, shifts in the zooplankton community composition or changes in the temperature regime experienced only provide clues about the processes that may be involved in the decline in recruitment. Both of these factors have the potential to affect survival rates of fish larvae either directly or indirectly by affecting growth rates (Leggett and DeBlois, 1994, Houde 2002). Such a link between the growth rates of herring larvae in the North Sea and their survival was recently demonstrated by Payne *et al.* (2013). However, without direct evidence of a change in diet composition or food intake, it is not clear exactly how or whether these changes in the plankton community might have been involved in the changes in recruitment.

Heath and Nicoll (1991) investigated the relationship between helminth parasite infection and feeding incidence in herring larvae from the 1987 year class in the North Sea. They found significantly lower feeding incidence in herring larvae infected with larvae of tetraphyllidean cestodes (*Scolex pleuronectes*) and suggested that the survival of herring larvae could be impacted as a consequence. However, the year class they investigated did not suffer from low survival and they suggested that population level effects could possibly be observed at very high prevalence.

The potential for parasites to act as major regulators of animal populations has been well described (May, 1983; Minchella and Scott, 1991). They can affect their host organism in many ways, including altering their behaviour (Lafferty and Morris, 1996) and competing with them for nutrients. Additionally, their presence and activities can lead to physical damage to the host (Rosenthal, 1967; Ivanchenko and Grozdilova, 1985). All these effects can lead to lower survival through decreased growth rates, severe physical damage, or by exposing the host to increased predation risk.

Herring larvae are infected with tetraphyllidean cestode larvae through the ingestion of infected copepods (Rosenthal, 1967; Marcogliese, 1995). The adult cestodes are generally restricted to elasmobranch fish and herring larvae are only one of many intermediate hosts for this parasite (Marcogliese, 1995). Both Heath and Nicoll (1991) and Rosenthal (1967) reported an increase in the intensity of parasite infection with increasing size of herring larvae indicating that the infection accumulates over time. Rosenthal (1967) did not observe any obvious detrimental effects on the herring larvae at relatively low intensities of infection in an aquarium experiment, but did notice that one herring larvae with a heavy infection (8 parasites) was impeded in its swimming ability.

Parasites such as tetraphyllidean cestode larvae, which are acquired through the diet and are relatively benign, accumulate in host populations and individuals and can therefore provide an index of cumulative feeding history (Campbell *et al.*, 1980; Williams *et al.*, 1992). High prevalence of infection is acquired, therefore, either through a generally higher intake of food in high prevalence years or a proportionally higher intake of infected prey.

Digenean trematodes are also commonly found in herring larvae (*Brachyphallus crenatus*, Ivanchenko and Grozdilova, 1985; *Lecithaster gibbosus*, Tolonen and Karlsbakk, 2003; *Hemiurus* sp., Karlsbakk *et al.*, 2003 and Heath and Nicoll, 1991, *Derogenes varicus*, Karlsbakk *et al.*, 2003). The primary host of digeneans is a mollusc from which free swimming cercaria are released to infect intermediate hosts, typically calanoid or harpacticoid copepods (Køie, 1979, 1989, 1990, 1992), which are the main prey of herring larvae (Checkley, 1982; Cohen and Lough, 1983; Munk, 1992). Some digenean trematodes such as *D. varicus* grow and feed inside herring larvae but do not typically reach maturity in this host, whereas others such as *Hemiurus* sp. can grow to maturity and reproduce in herring larvae (K. Mackenzie, unpublished data). Heath and Nicoll (1991) rarely found an intensity of digeneans exceeding one and observed no increase with the length of larvae and therefore no accumulation of parasites over time. Their conclusion was that herring larvae were only exposed to the infective stages of the digeneans for a brief period. However, a similar pattern would be observed if the accumulation of parasites in the herring larvae was detrimental and larvae with heavier infection were removed from the population. Such a scenario is supported by Ivanchenko and Grozdilova (1985). They reported detrimental effects on White Sea herring larvae from the digenean trematodes *L. gibbosus* and *B. crenatus*. The parasites damaged the mucous membranes of the herring intestines, causing embolisms which ultimately inhibited the passage of food, resulting in cessation of feeding and death.

Given the different patterns of infection and pathogenicity of tetraphyllidean cestode and digenean trematodes in larval herring, it is likely that their incidence provides different information on the feeding ecology of the host. Digeneans would be expected to have a negative effect on feeding success and therefore potentially on survival. In contrast, tetraphyllidean cestode larvae should have less direct impacts on survival and instead provide insights into feeding conditions experienced over the lifespan of the herring larvae.

The aim of this study was to investigate some of the mechanisms related to food consumption by which survival of herring larvae may have changed over 12 years, spanning periods of both good and poor recruitment. Key to our approach was the fact that larvae feeding in the wild coincidentally acquire gastroenteric parasites. The different behaviours and pathogenicity of parasite species means that their incidence can potentially be used to infer patterns of food intake and survival. If helminth parasite infection plays a role in the recent poor recruitment of North Sea herring, through a reduction in feeding incidence as suggested in Heath and Nicoll (1991), we would expect to see a difference in the pattern of parasite infection between years of high and low overwinter survival of herring larvae.

Material and methods

Selection of herring larvae specimens

Since 1977, late stage herring larvae in the North Sea have been surveyed as part of the ICES coordinated International Bottom Trawl Survey (IBTS, ICES, 2006). The synoptic survey is carried out by research vessels from participating institutes during late January and February, and measures abundance of herring larvae using a 2 m ringnet, the Methot–Isaacs–Kidd net (ICES, 2006). This component of the IBTS survey is commonly referred to as the MIK survey in reference to the net used.

Archived specimens of formaldehyde preserved herring larvae caught during the Marine Scotland Science (MSS) contributions to the ICES MIK surveys in February were available to this investigation. The samples were collected in the northwestern North Sea (Figure 1) and provided an opportunity to investigate stomach contents and infection with intestinal parasites over a succession of years with varying levels of overwinter survival. We chose to focus our study on herring larvae collected during the period 1995–2007 (1994–2006 year classes) to cover both the most recent period of poor survival (2002–2007) and a period before this with "normal" survival in the North Sea as a whole (1995–2001, Payne *et al.*, 2009).

The key feature of our study was the analysis of diet composition and gastroenteric parasite incidence between different years. However, parasite infection and feeding by herring larvae has been shown to vary geographically and with body size (Heath *et al.*, 1989; Heath and Nicoll, 1991; Munk, 1992; Busch, 1996). Hence, to avoid confounding our results with these factors, it was necessary to restrict our analysis to larvae from a standardized geographical area and size range.

A geographical subset of the available samples was defined such that in every year, there were >100 specimens of larvae available for analysis from a common set of ICES statistical rectangles. The area within which these samples were collected was referred to as the "study area". Within this geographical subset, the abundance in 1 mm length classes was extracted from the MIK survey database for the Scottish component and the median and quantiles calculated for each year. We selected a common length interval for examination that was contained within the 5th and 95th quantiles in every year and spanned the median of the length distribution for the majority of years.

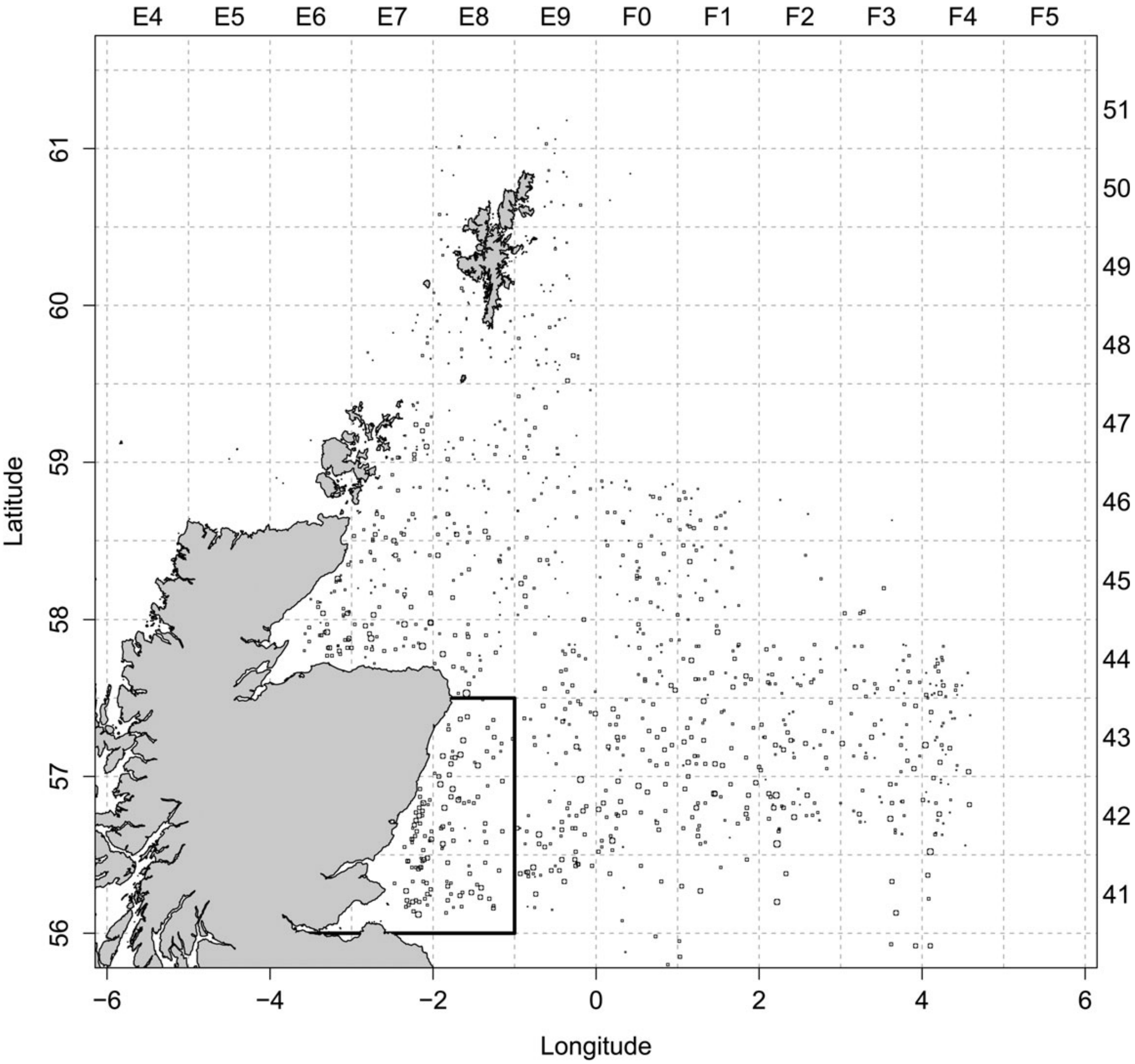

Figure 1. Location of study area in the northwestern North Sea off north-eastern Scotland and position of all hauls taken during the MSS component of the MIK survey in January–February between 1995 and 2007. Bubble radius is proportional to the number of larvae caught in each haul with the largest size corresponding to 510 larvae.

The formaldehyde-preserved specimens of larvae from the geographical subset were rinsed thoroughly in water and measured to the nearest millimetre. Only larvae within the chosen length range were subsequently dissected. The entire digestive tract was removed under a dissecting microscope with needles and placed in a drop of a mixture of water and glycerine (50/50 mixture) for easier handling. Only digestive tracts that were found to still be intact after extraction were examined further.

Prey items and parasites were extracted, identified, and measured as they were encountered. All parasites were photographed and identification of type specimens was confirmed by an independent expert (K. MacKenzie, University of Aberdeen, pers. comm.).

Herring larvae survival

Two internationally coordinated surveys provide global indices of abundance of herring larvae in the North Sea both before and after the winter period.

The ICES International Herring Larvae Survey (IHLS) is carried out in autumn (September–October) and winter (December–January) each year and samples larvae with a fine-mesh plankton net (250 μm mesh) at predetermined stations covering the main spawning areas: Orkney-Shetland, Buchan, Central North Sea, and Downs (Figure 2, Heath, 1993). The herring larvae caught in each haul are counted and measured to the nearest millimetre below, and the data are processed to estimate the abundance

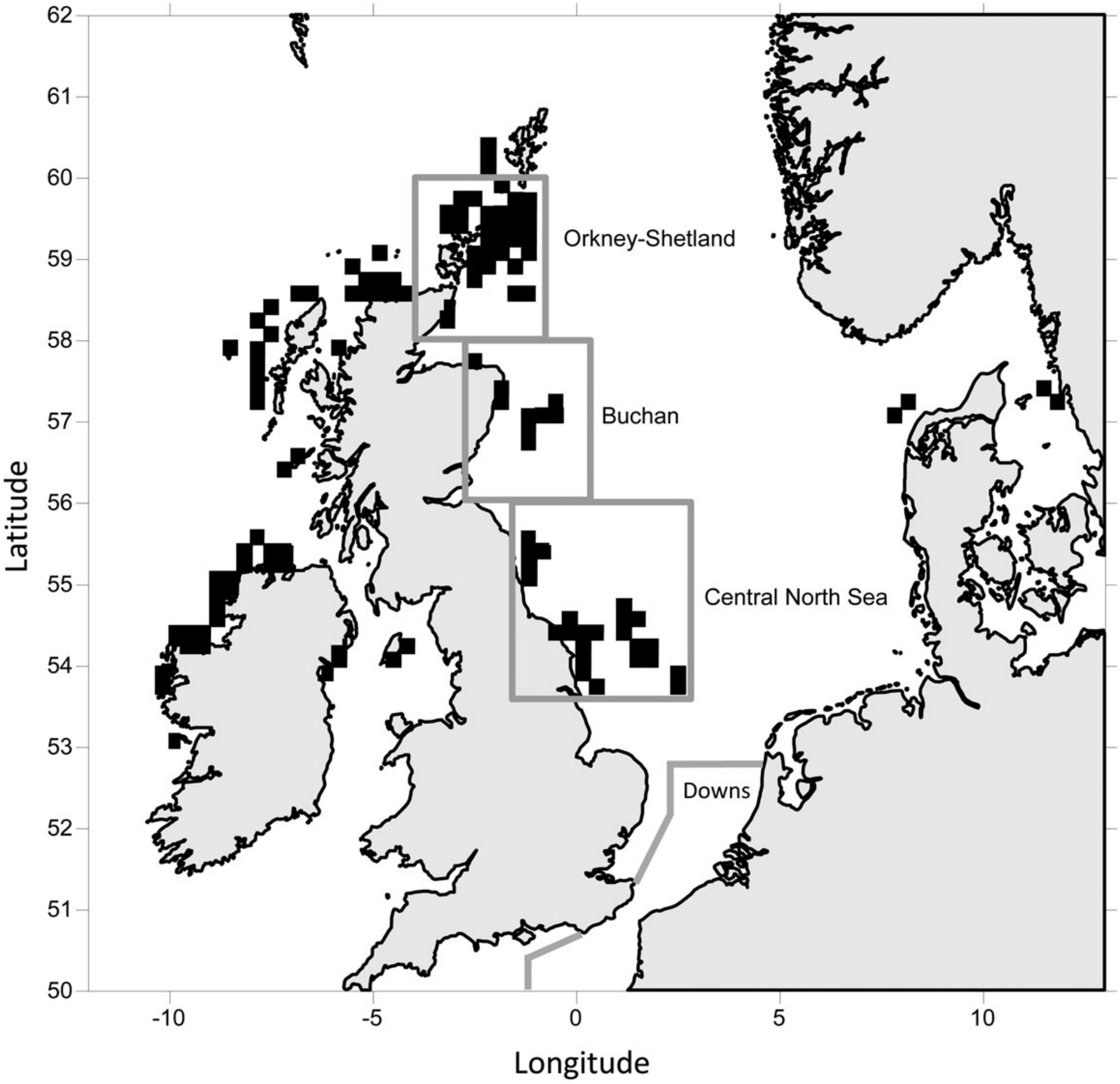

Figure 2. Locations of North Sea herring spawning distribution in autumn (August to September in Orkney-Shetland, Buchan, and Central North Sea) and winter (December–January in Downs) determined from catches of yolk-sac herring larvae, ripe fish, and haddock with herring eggs in the stomach (Based on Heath and Richardson, 1989). In the particle simulations, particles were released from all areas marked in black corresponding to known autumn spawning locations. Grey rectangles shows the delineation of North Sea herring spawning components as defined in the International Herring Larvae Survey. No particles were released within the Downs component area.

(number m^{-2}) of newly hatched larvae (<10 mm length) for each ICES statistical rectangle (1° longitude × 0.5° latitude). For each of the four sampling units (Figure 2), a larval abundance index (LAI) is calculated by summing the larval abundances for all rectangles contained in the unit. Difficulties in interpreting this time-series due to missing observations, high sampling noise, and differences in the spawning intensity between surveys (ICES, 2013) have led to the development of the spawning component abundance index (SCAI, Payne, 2010). The SCAI is a statistical model designed to analyse the LAI's from the IHLS and provides an index of abundance of newly hatched larvae for each of these spawning components. The SCAI has been shown to be robust to the challenges posed by the LAI time-series and the index has been used in the assessment of North Sea herring since 2012 (ICES, 2013).

Over the winter period, the developing herring larvae disperse with the prevailing currents to a potential North Sea-wide distribution. In the late winter, a second survey of these surviving herring larvae is carried out. This is the MIK survey mentioned above and it covers the whole of the North Sea during late January and February. The abundance index resulting from this survey—the IBTS0 index—is expressed as total abundance of late stage herring larvae in the North Sea and is used as a recruitment index in the assessment of North Sea herring (ICES, 2013).

These two surveys cover the entirety of the known distribution of both newly hatched and late stage larvae of North Sea herring. Abundance of late stage larvae in late winter at any point in the North Sea is a function of larval production in spawning areas in autumn, dispersal of the larvae, and mortality during the intervening period. The proportional relationship between the SCAI for all spawning components and the IBTS0 index therefore provides an index of survival of herring larvae over the winter period on a North Sea-wide scale. We calculated a North Sea-wide survival index for the study period (1995–2007) as a straight ratio between the sum of SCAI for all four spawning components (from Payne, 2013) and the IBTS0 index (from ICES, 2013, Table 2.3.3.1).

Local survival index

The North Sea-wide survival index however does not automatically apply to our local study area. Because the study area covered only a fraction of the total distribution of both early and late stage larvae, and because distribution of early and late larvae is not uniform throughout the North Sea (ICES, 2008), it was necessary to calculate a local index of survival that took account of dispersal patterns.

The dispersal of larvae was accounted for using a particle tracking model to estimate the proportional contribution of the different spawning components to the abundance of larvae in the study area in February. The SCAI for each of these individual spawning components provided the magnitude of larval production in these spawning areas and it was then possible to calculate an index of expected abundance in the study area in February if no mortality was experienced along the advection paths. The actual abundance of larvae in the study area in February was calculated from the MIK survey hauls from the study area for each year. The proportional relationship between the observed actual and the modelled expected abundance was taken as an index of survival. The index was not considered to be an absolute estimate of the mortality rate each year, but was used to compare relative local survival among years.

The Buchan spawning area was not surveyed in 1994 and 1995 and the level of uncertainty for the Buchan component of SCAI for these 2 years is almost double of that for the remaining series as a consequence (Payne, 2010). We felt unjustified to use these modelled values without any underlying observations for those 2 years in the Buchan component SCAI. It was thus not possible to estimate the survival of herring larvae in the study area for 1994 and 1995.

Particle tracking

The particle tracking model was based on methods described by Heath and Gallego (1998). The basis of the model was that year-specific daily horizontal flowfields were produced by the SNAC model (Logemann *et al.*, 2004), forced with atmospheric pressure data extracted from the ECMWF Operational Analysis dataset (ECMWF 2006–2008). The horizontal resolution of the model was 0.125° latitude by 0.250° longitude, which corresponds to a distance of 13.9 km in latitude and ∼13.5–15.5 km in longitude over the domain of interest. The model was run for the period mid-September (day 258, or 15 September) to the end of February (168 days duration) in each of the start-years 1994–2006.

Particles were released from all "wet" (i.e. water depth >0 m) start positions on a 5 × 5 km grid covering all the known autumn spawning areas of herring identified in Heath and Richardson (1989) in both the North Sea and to the west of Scotland (Figure 2). No particles were released in the Downs area as the timing (December/January) and the location of spawning of this component makes it unlikely that larvae with this origin should be present in our study area as demonstrated by hydrographic modelling in Dickey-Collas *et al.* (2009).

Twenty-five particles were released from each start location, each of which had the potential to follow a unique trajectory due to the effects of horizontal diffusion which was parameterized as a stochastic process in the model. A total of 148 625 particles were released over all areas. Although 25 particles per release location was the maximum we could use within the constraints of our computing hardware, exploratory sensitivity analyses suggested that an adequate number of particles was $n < 50$ (see Gallego, 2011). In addition, we carried out a number of identical simulations (using 1994 flowfields) and estimated that, for that number of particles, the coefficient of variation resulting from stochastic processes was ∼8%.

The tracking time-step was 1 h and particle positions were stored daily. All particles migrated with a sinusoidal diel vertical migration pattern between 5 and 45 m depth. The number and origin of particles reaching the study area within the month of February were extracted from the dataset of daily tracks of all simulated particles (Figure 3). To account for differences in abundance of larvae between different years and spawning areas, particles were weighted with the year- and area-specific SCAI at their origin. Interannual differences in the (unweighted) number of particles reaching the target area were the result of interannual differences in transport patterns from each spawning area, while interannual differences in the (weighted) simulated larvae abundance index were the result of the combination of interannual differences in transport patterns from each spawning area and annual differences in their respective SCAI-derived weighting. The total number of expected arrivals could not be calculated for 1994 and 1995 due to the lack of surveying in the Buchan area as mentioned above.

Observed abundance of late stage larvae in February

An annual abundance index for late stage herring larvae in the study area was calculated based on samples of herring larvae taken within the limits of the study area during the ICES MIK survey in February,

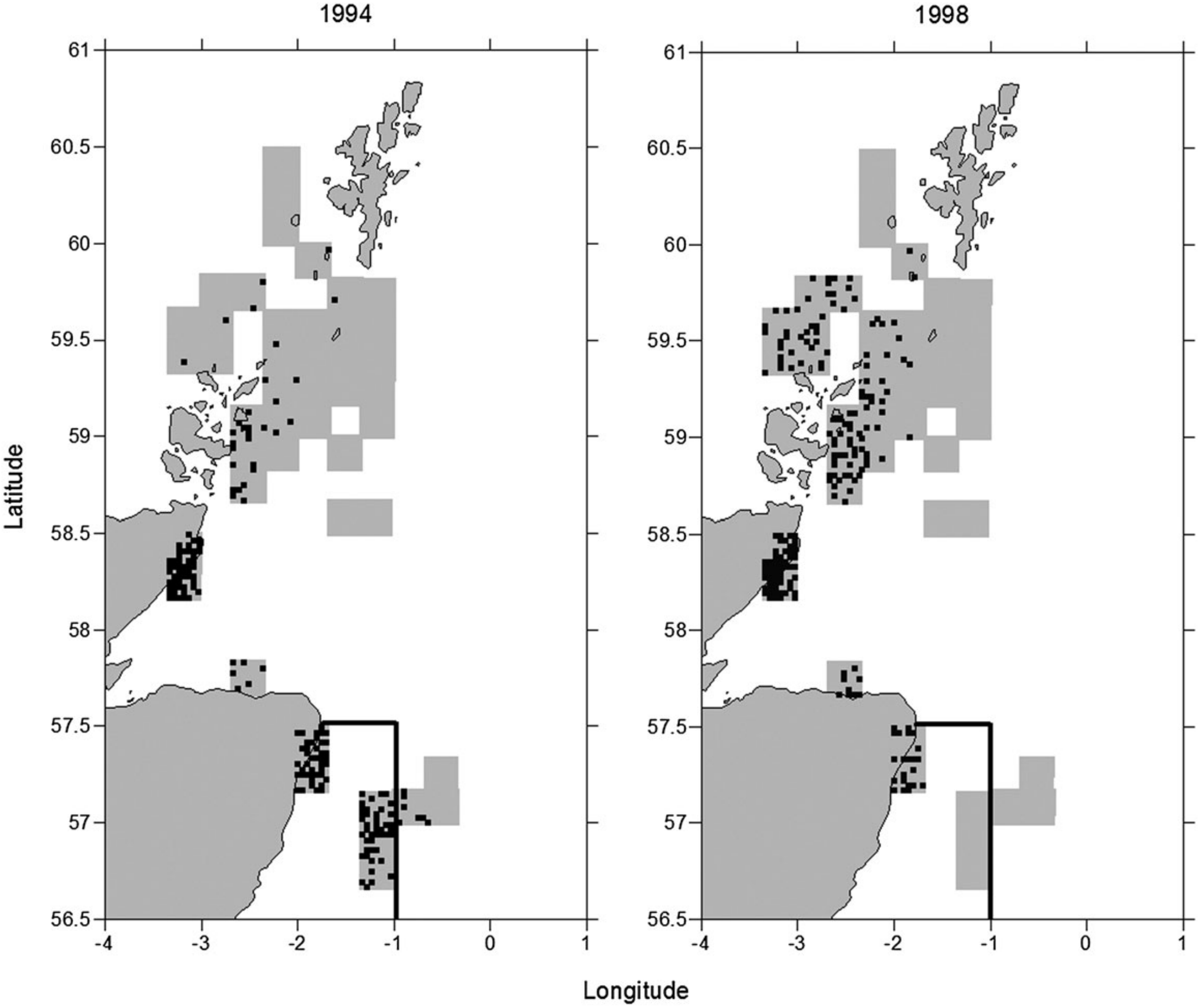

Figure 3. Results from particle tracking simulations for particles released on 15 September from known herring spawning grounds in the North Sea between 1994 and 2006. Example of two contrasting years (left: 1994 spawning; right: 1998 spawning) when particles recorded within our study area at any time during February originated from quite different source locations. Spawning grounds (particle release areas) are represented by grey shading on the maps. Black dots represent the origin of the particles that subsequently reached our study area (outlined in black).

including only samples with the mean larval length of 20 mm or more. This follows the procedure used to produce the IBTS0 abundance index of late stage herring larvae for the North Sea, based on these same surveys (ICES, 1996). The mean abundance per square metre was calculated for each sampled ICES rectangle within the study area and this number was raised by the "wet" surface area of the corresponding rectangle to obtain a total number of larvae per rectangle. The total number of larvae was summed over all rectangles surveyed and divided by the number of rectangles surveyed to obtain the mean number of larvae per surveyed ICES rectangle. The total number of larvae in the study area was obtained by multiplying the mean number of larvae per surveyed ICES rectangle with the number of ICES rectangles in the study area ($n = 5$).

Data analysis

Survival and parasites

We tested whether the survival of herring larvae was influenced by the prevalence of tetraphyllidean and digenean parasites by fitting a general linear model (lm function in R version 3.0.1) to the data with log-transformed survival modelled as a response and tetraphyllidean and digenean prevalence as independent variables. Survival was log-transformed to satisfy the assumption of normality of residuals and diagnostics plots confirmed constant variance with the mean after transformation. The best fitting model was selected by comparing the Akaike information criteria corrected for sample size (AIC_c) and the adjusted R^2-values for the models.

Feeding incidence

We tested the hypothesis that feeding incidence of herring larvae in the study area was similar for larvae with and without parasites. Feeding incidence was measured by the presence or absence of prey items in the herring larvae and larvae were characterized as having either no parasites, digenean trematodes, or tetraphyllidean cestode larvae present in the intestine. To take into account the anticipated effect of time of day of capture on feeding incidence,

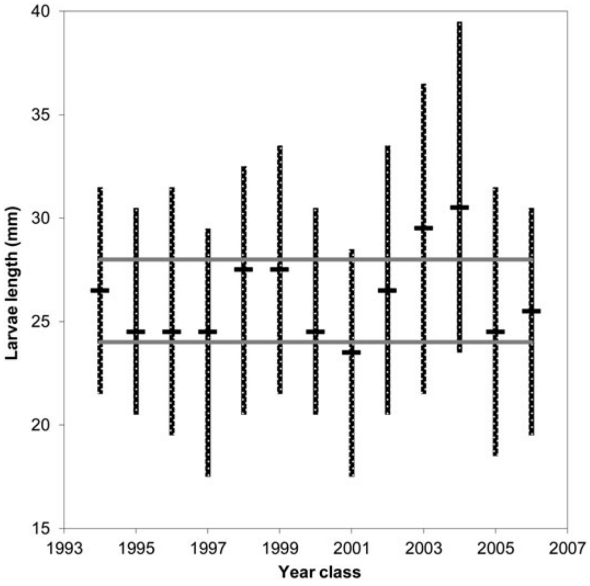

Figure 4. Yearly length distribution of herring larvae caught in the study area on the MSS component of MIK surveys between 1995 and 2007 (year classes 1994–2006). Median length is represented by the short horizontal bars and the error bars extend from the 5th to the 95th quantile. The long horizontal bars at 24 and 28 mm represent the minimum and maximum length of larvae selected for use in this investigation.

we included this parameter in the model as time-lag from sunset to capture time.

Given the sampling structure of this study and the patchy distribution of both larvae and prey in the environment, larvae captured in the same haul would potentially have been subject to more similar feeding conditions than larvae coming from different hauls. Larvae captured from the same haul were therefore considered pseudo-replicates of that haul. To account for this, we used a generalized linear mixed-effects model (binomial distribution, logit link function, lme4 package in R version 3.0.1, Bates *et al.*, 2013) with haul included as a random effect to assess how the parasite state of the larvae influenced the likelihood that the larvae had been feeding (GLMM-parasite).

The model was validated following the guidelines provided by Bolker *et al.* (2009).

Results

Study area and length ranges of larvae

When aggregated over all years in the period 1995–2007, the MSS component of MIK surveys in February showed that herring larvae were concentrated in the coastal strip (25–35 km wide) along the northeast of Scotland and in a band stretching eastwards across the North Sea between 56 and 57°N. However, there was considerable interannual variability in this pattern, and when this was taken into account the area where larvae were most consistently caught was between 56 and 57.5°N, between the coast and 1°W (Figure 1). This area (the study area) defined the geographical subset of samples used in the project.

Within the study area, the length distribution of larvae in February varied between years (Figure 4), with larvae from the 2003 and 2004 year classes being particularly large, and those in 1997 and 2001 year classes being particularly small. These differences imply differences in growth rate between years, or differences in age at capture, or a combination of the two. Differences in growth rate and age at capture could reflect variations in the hatching origin of larvae. A length interval of 24–28 mm met the criteria for defining a subset of lengths to be examined for gut contents (i.e. spanned the median in all but 3 years and was contained within the 5th and 95th quantiles in all years).

Particle tracking and survival

The spatial distribution of particle releases was constant from year to year, reflecting the fixed locations of spawning grounds. However, the locations of release sites that produced particles which arrived in the study area off the east coast of Scotland in February varied from year to year, reflecting interannual variations in the transport patterns (Figure 3). It is worth noting that all particles that reached the target area in the month of February originated from the Orkney-Shetland and Buchan spawning areas (41 950 and 10 675 particles released yearly, respectively).

The total number of particles recorded in the study area during February showed marked differences between years (Figure 5a). The year- and area-specific SCAI also varied among years and between the two areas contributing particles to the study area (Figure 5b). Overall, the Orkney-Shetland spawning area contributed the largest amount of simulated larvae to the study area in all years (79.5–99.0%) with a peak in contribution from the Buchan spawning area for the 2002 year class (Figure 5c).

The expected total abundance of herring larvae in the study area based on these model results varied between years with a prominent peak in the 2002 year class (Figure 6a). This variation could not be attributed solely to either of the two sources of variation examined with the particle drift simulation but was the result of both interannual differences in transport pattern and area- and year-specific differences in larval production.

The observed abundance in February in the study area, calculated from local survey data, also varied among years, with higher values in the early part of the study period and again in the last 2 year classes (Figure 6a). The resulting clear variation in survival among years of herring larvae caught within the study area was adequate for investigating the relation between survival and potential causal factors (Figure 6b).

In contrast to the North Sea-wide survival, which was consistently low for all year classes between 2002 and 2006 (Figure 6b), the local survival index was more varied and shows increasing survival of the two latest year classes investigated. While numbers of herring larvae in the MIK surveys remained low for the North Sea as a whole, the proportion captured within the study area increased considerably in the last years included in this analysis, accounting for up to 28% of the total population in the North Sea (Figure 7).

Herring larvae feeding and diet

We dissected a minimum of 30 herring larvae per year for the period 1995–2007 (1994–2006 year class), adding up to a total of 454 larvae for the study. Parasite and prey incidence was recorded for all 454 larvae dissected. For the majority of the larvae, a full analysis of gut content was also carried out. For 21 of the dissected larvae, only parasite and feeding incidence was noted (Table 1).

A total of 1641 prey items were identified from the dissected intestines (Table 1). Over the entire study period, small calanoid copepods (31%), the cyclopoid *Oithona* spp. (38%), and copepod nauplii (12%) dominated the diet by numbers. This highlights the importance of small copepods in the diet of herring larvae

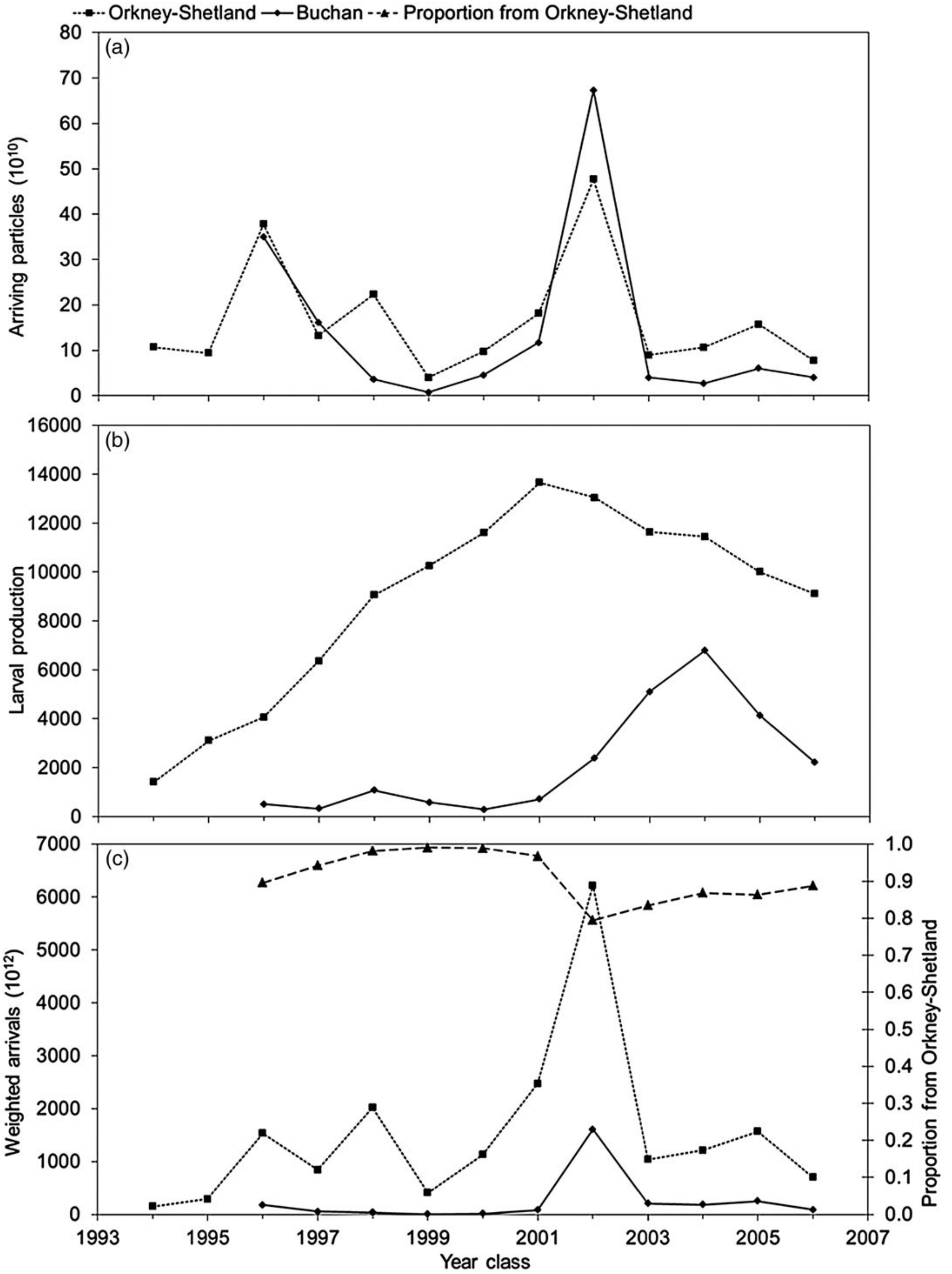

Figure 5. (a) Number of particles representing herring larvae modelled to have arrived in study area during February after release on 15 September in the previous year in Orkney-Shetland and Buchan spawning areas. (b) Size of larval production in Orkney-Shetland and Buchan spawning areas given as SCAI. (c) Relative number of larvae expected to arrive in study area from Orkney-Shetland and Buchan spawning grounds as number of particles arriving weighted by size of larval production at the origin (SCAI). Proportional contribution of the Orkney-Shetland spawning area is also indicated. Year class refers to the year particles were released, i.e. when larvae hatched.

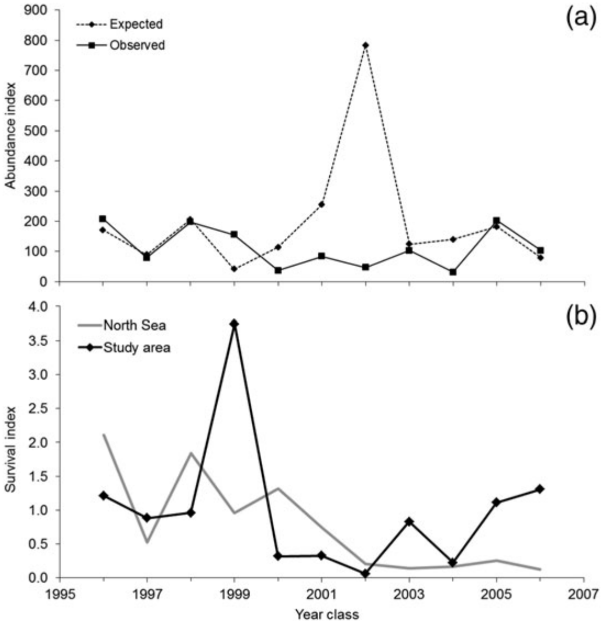

Figure 6. (a) Indices of expected abundance of herring larvae in study area (assuming no mortalities sustained during drift phase) based on particle tracking model (abundance $\times 10^{13}$) and the actual observed abundance in study area calculated from the MIK survey data (abundance $\times 10^{8}$). (b) Indices of survival in the study area, calculated in this study, and the entire North Sea expressed as a ratio between the summed SCAI's and the IBTS0.

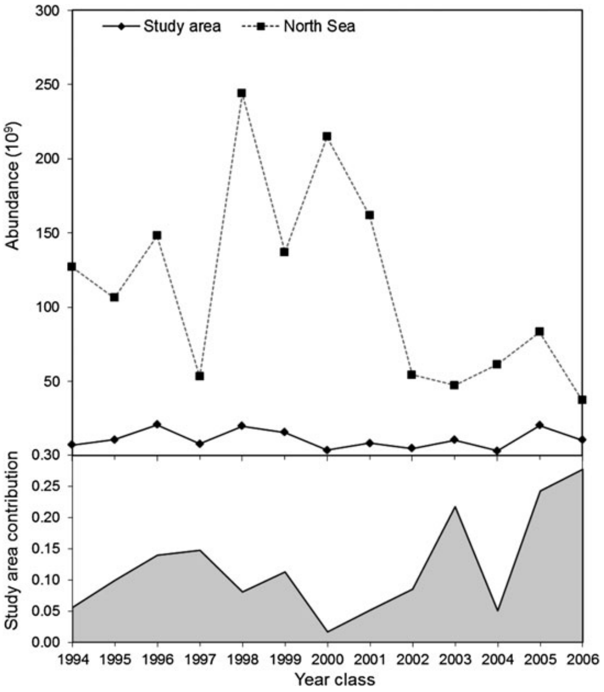

Figure 7. Total abundance of herring larvae in North Sea, the IBTS0 index, and in study area during MIK surveys in the North Sea between 1995 and 2012 (1994–2011 year classes). Lower panel indicates proportion within study area.

in the study area. The calanoid copepods were almost entirely *Paracalanus* sp. (50%), *Pseudocalanus* sp. (21%), and *Acartia* sp. (8%).

Prey items were observed in 117 (26%) of the guts examined. This proportion varied widely among years between 0 and 80%, resulting in very little or no data available for some years with respect to food composition (Table 1). Since herring larvae are visual predators and generally do not feed at night, the incidence of prey items in the guts was expected to decline with time after sunset. For some years, all samples in the study area were taken very late in the night and for these years, very few larvae had any prey items in them (1994 and 1997 year class in particular, Table 1). The very small proportion of guts containing prey items in these years made it inappropriate to perform further detailed analyses regarding changes in prey composition among years.

Parasites in herring larvae

Two types of parasitic helminths were found in the intestines of the larval herring. One was a digenean trematode (*D. varicus*) and the other was larvae of tetraphyllidean cestodes otherwise known under the species complex *Scolex pleuronectis*. The prevalence (proportion of larvae carrying parasites) of both parasite types showed marked variation among years ranging from 0 to 0.35 for digeneans and 0.03 to 0.33 for tetraphyllideans (Figure 8). The mean prevalence over the entire study period was higher for tetraphyllideans (0.15 ± 0.05) than for digeneans (0.09 ± 0.05). The intensity (number of parasites per larvae) of digeneans only ever exceeded one in the 1999 year class, whereas it was common to find several tetraphyllideans in a single herring larva, with three being the maximum observed (Figure 8). The intensity of infection of tetraphyllideans seemed to be higher in year classes with high prevalence. The two types of parasites were co-occurring in seven herring larvae (Table 2). This was considered too few to justify inclusion as a category in the analysis, but since there was no information available as to the possible effects of the two parasite types being present simultaneously in one larva, these were excluded from the subsequent analyses on the effects of parasites on herring larvae feeding and survival.

Survival and parasites

We tested the hypothesis that survival of herring larvae was influenced by the prevalence of tetraphyllidean and digenean parasites. A model including an effect of the interaction between the two parasite species in Table 3 was the best fitting model based on the AIC_c. This best fitting model indicated that digenean prevalence had a negative effect on survival and that there was a significant positive interaction between tetraphyllidean and digenean prevalence (Table 4). The model provided a good fit to the data and explained 53% of the variation in survival (Table 3). There was little support to keep the main effect of tetraphyllidean prevalence in the model (Table 3). The fitted model met the assumptions for general linear models (Figure 1, Supplementary data).

The significant interaction between the prevalence of the two parasites indicates that the effect of the digenean parasite on survival depends on the level of tetraphyllidean prevalence (Figure 9). When the prevalence of tetraphyllideans was low, there was a strong negative effect of digenean prevalence on survival, but with increasing prevalence of tetraphyllidean cestodes, this negative effect was eliminated and at higher levels of tetraphyllidean prevalence, there was no effect of prevalence of either parasite on survival (Figure 9).

Feeding incidence

We also tested the hypothesis that feeding incidence of herring larvae in the study area was similar for larvae with and without parasites using a generalized linear mixed-effects modelling approach.

Table 1. Analysis and feeding information (four top rows), and number of prey items by year and type found in herring larvae captured between 1995 and 2007 (1994–2006 year classes).

	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Total
Larvae dissected	30	32	83	34	31	31	31	30	30	30	32	30	30	454
Larvae with prey	0	15	17	1	9	8	9	10	5	12	2	5	24	117
Feeding incidence (%)	0	47	20	3	29	26	29	33	17	40	6	17	80	26
Larvae with full prey identification	0	15	17	1	9	8	9	10	2	11	1	5	8	96
Calanoid copepods		77	78	0	5	8	47	54	11	60	5	102	62	509
Cyclopoid copepods		106	105	0	52	21	37	68	7	94	0	109	25	624
Harpacticoid copepods		0	0	0	0	0	0	1	0	0	0	0	0	1
Poecilostomatoid copepods		0	13	0	2	0	1	0	0	0	0	0	3	19
Copepod unspecified		1	3	0	3	1	2	10	0	7	0	15	9	51
Nauplii		58	40	0	41	0	5	9	1	34	0	0	4	192
Isopoda		0	0	0	1	0	0	0	1	0	0	0	0	2
Crustacean remains		1	0	0	2	0	0	2	0	0	0	0	1	6
Eggs		7	8	0	28	2	8	8	1	0	0	3	8	73
Molluscs		3	42	0	59	1	1	1	0	2	0	1	3	113
Unidentified prey		10	0	1	12	7	0	7	0	3	0	3	8	51
Grand total		263	289	1	205	40	101	160	21	200	5	233	123	1 641

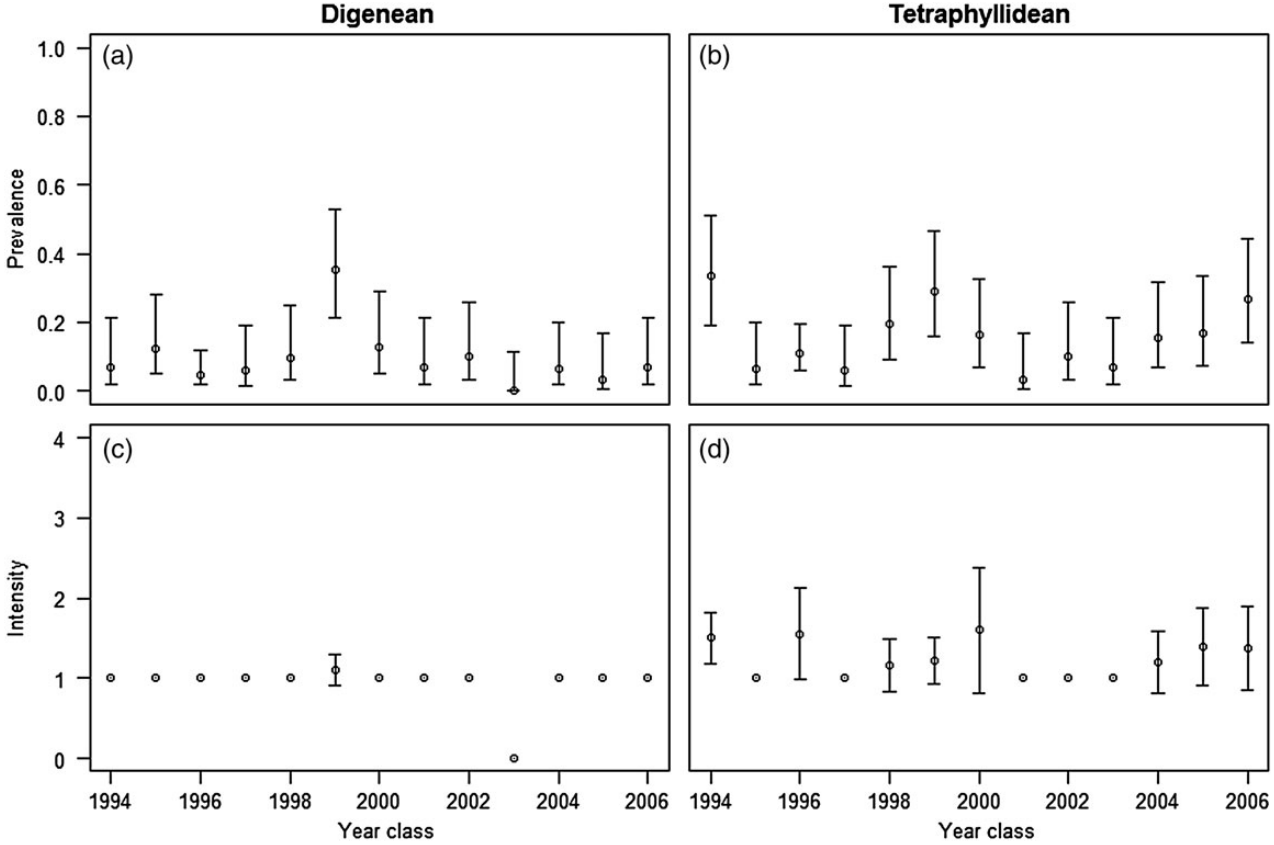

Figure 8. Prevalence and intensity of digeneans (a and c) and tetraphyllidean larvae (b and d) in herring larvae collected in the study area between 1995 and 2007 (year classes 1994–2006). Prevalence in this figure refers to the proportion of individuals investigated that are infected, and intensity meaning the average number of parasites encountered in infected individuals. Error bars represent 95% confidence intervals. The 95% confidence intervals for prevalence were calculated using Wilson's score method without correction for continuity (Newcombe, 1998).

With a ratio of residual deviance to residual degrees of freedom of 0.75 ($\chi^2 = 332.5$, d.f. $= 442$, $p = 1$), the model was not found to be overdispersed. The residuals pattern was investigated using the "binnedplot" function in the "arm" package in R (Gelman and Su, 2013). The binned Pearson residuals showed no distinct pattern against the residual values.

Once the random effect of haul had been accounted for, we found that feeding incidence did indeed significantly decrease with time from sunset (Table 5 and Figure 10). In addition, parasite presence influenced feeding incidence and the direction in which likelihood of feeding was affected differed with the type of parasite (Table 5). There was some indication that larvae infected with digenean

Table 2. Annual summaries of parasite prevalence in herring larvae collected in the study area between 1995 and 2007 (1994–2006 year classes).

Year class	Larvae sampled	Number infected		Prevalence		Joint occurrence
		Tetraphyllideans	Digeneans	Tetraphyllideans	Digeneans	
1994	30	10	2	0.33	0.07	1
1995	32	2	4	0.06	0.13	0
1996	83	9	4	0.11	0.05	0
1997	34	2	2	0.06	0.06	0
1998	31	6	3	0.19	0.10	1
1999	31	9	11	0.29	0.35	2
2000	31	5	4	0.16	0.13	2
2001	30	1	2	0.03	0.07	0
2002	30	3	3	0.10	0.10	1
2003	30	2	0	0.07	0.00	0
2004	32	5	2	0.16	0.06	0
2005	30	5	1	0.17	0.03	0
2006	30	8	2	0.27	0.07	0

Table 3. Candidate linear models describing the relationship between survival of herring larvae and prevalence of two helminth parasites in the northwestern North Sea, 1995–2007.

Model	Model parameters	*F*-statistic	*p*-value	AIC$_c$	Adjusted R^2
1	log(survival) ~ ptet	$F_{1,9} = 3.04$	0.12	35.30	0.17
2	log(survival) ~ pdig	$F_{1,9} = 1.20$	0.30	37.13	0.02
3	log(survival) ~ ptet + pdig	$F_{2,8} = 1.36$	0.31	37.28	0.07
4	log(survival) ~ pdig × ptet	$F_{3,7} = 3.92$	0.06	31.66	0.47
5	log(survival) ~ pdig + pdig : ptet	$F_{2,8} = 6.59$	0.02	29.79	0.53

Survival was log-transformed to satisfy the assumption of normality and diagnostic plots confirmed constant variance with the mean after transformation. (pdig and ptet refer to the prevalence of tetraphyllidean and digenean parasites, respectively).

Table 4. Estimates, standard errors of the mean (s.e.), and significance of parameters of best fitting model in Table 3 (pdig and ptet refers to the prevalence of tetraphyllidean and digenean parasites, respectively).

Parameter	Coefficient	s.e.	*t*-value	*p*-value
pdig	−30.52	10.886	−2.80	0.02
pdig: ptet	114.51	35.013	3.27	0.01

trematodes were less likely to have fed than non-parasitized larvae. In contrast, there was strong support in the model that larvae carrying tetraphyllidean cestode larvae were more likely to have fed than non-parasitized larvae (Table 5 and Figure 11). It is worth noting that we obtained similar results using a generalized linear model approach. However, the significance of these effects was less pronounced given that pseudo-replication was not accounted for. In addition, a GLMM (not presented), which did not account for the fixed effect of parasite (GLMM-NOparasite), was not supported by the data when contrasted with the model above ($\text{AIC}_{\text{GLMM-parasite}} = 392.8$, $\text{AIC}_{\text{GLMM-NOparasite}} = 402.4$).

Discussion

The availability of archived herring larvae from a succession of years with both high and low recruitment of North Sea herring provided an opportunity to investigate a potential relationship between feeding, infection with intestinal parasites, and overwinter survival of herring larvae. The use of a biophysical model to factor out the direct effect of oceanographic transport variability allowed us to use early larval abundance survey data to account for interannual spawning variability and estimate reliable annual indices of survival for the relevant stocks.

A particle tracking modelling approach was used to identify the origin of the larvae sampled in the study area and to account for interannual transport variability. This methodology is critically dependent on the suitability of the underlying hydrodynamic model. SNAC (Logemann *et al.*, 2004) is a statistical representation of HAMSOM (Backhaus and Hainbucher, 1987) that has been used comprehensively for similar applications in the general domain of interest [e.g. see Gallego (2011) and references therein]. As a comparative exercise, we carried out a similar set of particle tracking simulations using a different hydrodynamic model (POLCOMS; Holt and James, 1999), though for a shorter time-series available to us (1994–2003). The new simulations (not presented here) resulted in the same origin of all larvae sampled in our study (Orkney-Shetland and Buchan) and a similar pattern of years with high and low transport success, although there were some differences in their relative magnitude and POLCOMS-based simulations resulted in a consistently higher (~3 times) number of particles reaching the target area. However, the latter would in effect act as a scaling factor which should not affect the statistical outcome of our analyses, which was the same for the common time-series. Therefore, we felt justified to use the SNAC-based simulations over the full series when survey and hydrodynamic model data were available to us (1994/1995–2006/2007).

The modelling approach also made a number of simplifying assumptions in the way herring biology was represented (for model sensitivity analyses, see Gallego, 2011). One important assumption was the selected particles release date (representing hatching date).

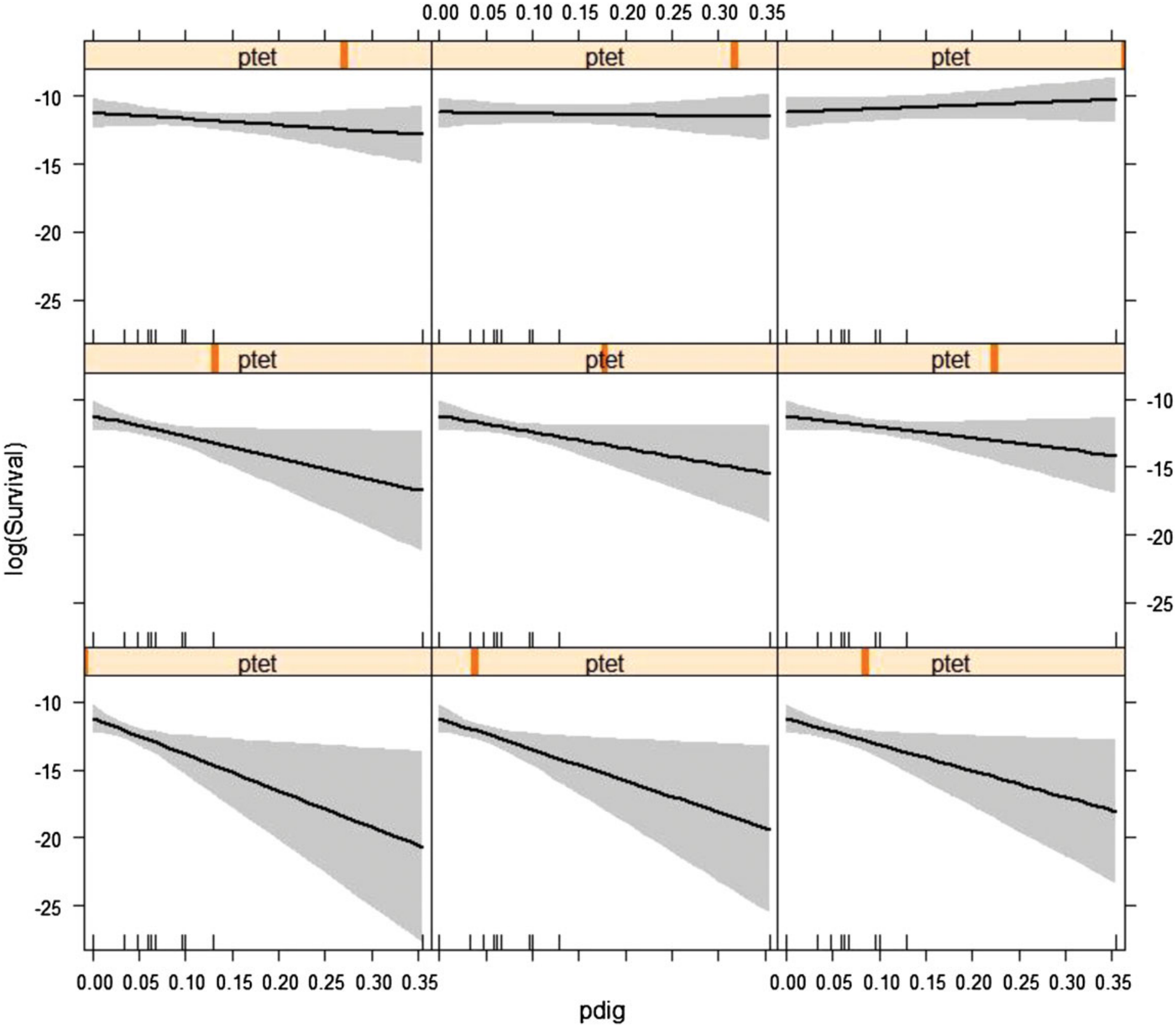

Figure 9. Interaction plot of the effect of prevalence of digenean (pdig) and tetraphyllidean (ptet) parasites on survival of larval herring in the northwestern North Sea. The plot shows the effect of digenean prevalence on log-transformed survival at different levels of tetraphyllidean prevalence.

Table 5. Contrasts summary estimates, standard errors of the mean (s.e.), and significance of parameters from the generalized linear mixed-effects model (prey present ~ state + sunset + (1 | haul), see text) describing the relationship between presence of two types of parasites on the likelihood of feeding in larval herring taking into account time of capture (hours after sunset) and haul effects.

Parameter	Estimate	s.e.	*Z*-value	*p*-value
State (no parasite)	0.41	0.458	0.89	0.37
State (digenean)	−1.30	0.647	−2.02	0.04
State (tetraphyllidean)	1.12	0.403	2.78	0.006
Hours after sunset	−0.45	0.0962	−4.70	<0.0001

The estimated variance for the random effect (haul) was 1.715 (44 hauls, 447 larvae), AIC = 392.8.

Herring spawning time varies between spawning stocks and, even within a given spawning stock, there is some interannual variability (Heath, 1993). However, in the absence of detailed multi-annual spatially and temporally resolved information on timing of spawning, it was unfeasible to incorporate spawning time variability into our model. Consequently, we selected a single larval hatch date (15 September) as a single particles release date from all spawning locations. For all areas that could contribute larvae to our study area, based on widely accepted oceanographic transport patterns, the west coast of Scotland herring stock spawns predominantly from August to October (Rankine, 1986), while spawning in the Orkney-Shetland area is from the end of August through September and in Buchan in September–October (Heath, 1993). In the years considered in our study, the larval surveys covering the Orkney-Shetland and Buchan areas were carried out in the second half of September. The particles release date of 15 September, therefore, allowed us to use the survey data as a weighting factor for spawning in our analysis. The average growth rates required for those larvae to reach the selected size interval of 24–28 mm in the month of February are 0.13–0.15 mm d^{-1}, which are well within the range reported in the literature (Lough *et al.*, 1982; Gamble *et al.*, 1985;

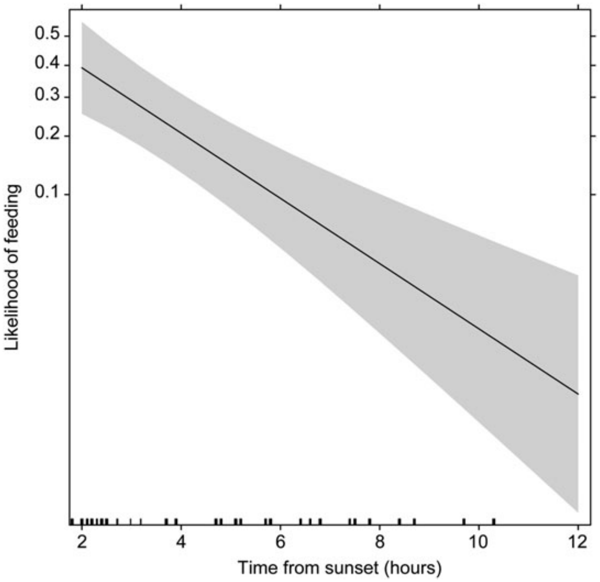

Figure 10. Predicted partial effect from the generalized linear mixed effects model (prey present ~ state + sunset + (1 | haul), see text) showing the significant negative effect of time-lag from sunset to capture time (time from sunset) on likelihood of feeding.

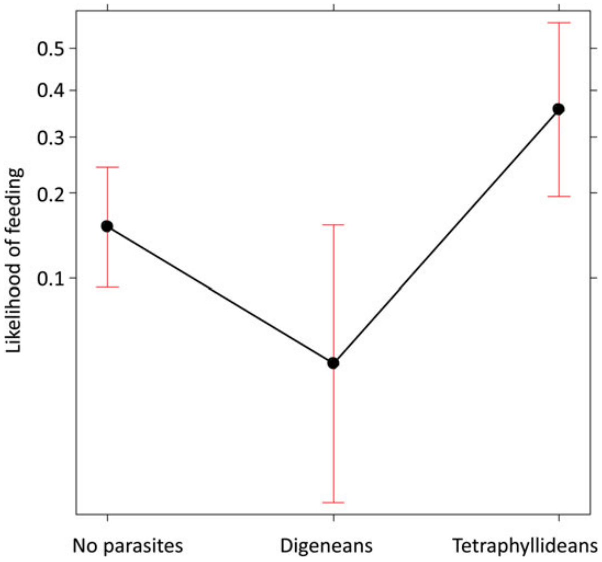

Figure 11. Predicted partial effects plot from the generalized mixed-effects model (prey present ~ state + sunset + (1 | haul), see text) showing the difference in likelihood of feeding between non-parasitized larvae and larvae carrying digeneans and tetraphyllideans. Vertical error bars represent 95% confidence intervals.

Geffen, 1986). The selection of a fixed length interval for all years may have introduced additional variability into our analysis, as this common range may have resulted in the selection of slower or faster growing components of the population, from year to year. However, the selected range was contained within the 5th and 95th quantiles every year and spanned the median of the length distribution for most years, thus minimizing this potential shortcoming. Additionally, selecting a variable length interval between years would have introduced additional ontogenetic diet variability effects.

At the basis of our investigation was the hypothesis that herring larval overwintering survival could be regulated by parasite infection. The two types of parasites, tetraphyllidean cestode larvae and digenean trematodes, which were identified from herring larvae digestive tracts, have previously been reported from herring larvae in the Northeast Atlantic and the North Sea (Rosenthal, 1967; Heath and Nicoll, 1991; Karlsbakk *et al.*, 2003; Tolonen and Karlsbakk, 2003). The prevalences and intensities we report are well within the range reported in these studies and the effects we describe here are therefore not the result of abnormally high or low levels of parasite prevalence or intensity. Our analyses indicate an interaction at the population level between the effects of the two parasites; the different way that these two types of parasites affect herring larvae may provide the explanation. Herring larvae survival is impacted by digenean parasites through the physical damage to individual larvae, affecting their ability to feed (Ivanchenko and Grozdilova, 1985). However, in years of good cumulative feeding conditions, as indicated by high prevalence of the relatively benign tetraphyllidean cestode larvae, the negative impact of the digeneans is offset by better survival of herring larvae overall. This scenario is further supported by the differences found in feeding incidence between the three categories of larvae. There was some indication that larvae with digeneans had lower feeding incidence than non-parasitized larvae, in agreement with the parasites causing physical damage inhibiting feeding. The larvae with tetraphyllidean cestodes, on the other hand, had significantly higher feeding incidence. Rather than being a direct consequence of the presence of the parasite, it is likely to simply reflect the better feeding conditions they have been subject to which in turn also caused the higher prevalence of tetraphyllideans.

In contrast to this study, Heath and Nicoll (1991) found lower feeding incidence in larvae infected with tetraphyllidean cestode larvae. However, they did not take into account in their analysis that feeding incidence might have been impacted by the time of day of capture of the larvae. We found a significant negative relationship between feeding incidence and the elapsed time between sunset and capture. This relationship is commonly described for herring larvae that are visual predators and rely on some level of light for effective prey capture (e.g. Cohen and Lough, 1983) and should be taken into account whenever feeding incidence is being used to measure feeding success (Llopiz, 2013). Similarly, gut evacuation at capture has the potential to influence feeding success estimates in herring larvae (Hay, 1981). In this study, we used simple presence/absence data to infer feeding incidence rather than number of prey items or stomach fullness, an index that is only sensitive to total evacuation of the gut during capture. In line with Heath and Nicoll (1991), we consider it unlikely that there is a difference in the incidence of full evacuation of stomachs between parasitized and non-parasitized larvae that could have biased our results.

Differences among years in tetraphyllidean and digenean prevalence in the herring larvae could simply reflect differences in the availability of infectious parasites in the zooplankton. If this is the case, there seems to be a link between factors influencing parasite availability, particularly tetraphyllideans, and herring larvae survival. The differences in circulation pattern and consequently transport patterns among years could be one such factor. A detailed investigation of the potential mechanisms causing such a link is beyond the scope of this paper, but could possibly further illuminate factors affecting the survival of herring larvae in the North Sea.

Although we did investigate diet of late stage herring larvae, the very low sample sizes and the paucity of data on diet for several of the years in our study period mean that the conclusions that could be drawn regarding the interannual differences in the importance of different prey is speculative at best. However, it is worth noting that in general, the food items that were abundant in stomachs in this study such as *Paracalanus* sp., *Pseudocalanus* sp., *Oithona* sp., and other small calanoid copepods have also previously been recorded as important food items for herring larvae in the North Atlantic (Schnack, 1972; Checkley, 1982; Cohen and Lough, 1983). In any case, the information on stomach contents collected from our samples provides only a snapshot in time of the diet and food consumption of the herring larvae immediately before sampling. However, larvae survival from hatching is a product of the integrated diet and consumption over many months. In this study, we have used data on benign parasites acquired through feeding to make inference regarding feeding of herring larvae over a much longer time-scale. The main diet items reported in this study are also the zooplankton groups that have been linked to the transfer of the parasites found in the herring larvae (Køie, 1979; Marcogliese, 1995), further supporting that these parasites are indicators of cumulative food intake.

Although our results support overwintering as a critical period for the survival of larval herring, it is not possible to test whether this corresponds to the onset of exogenous feeding, as in Hjort's "critical period" hypothesis (Hjort, 1914), or some other time during that stage. The exact time at which larvae are most affected is still unknown, since by analysing larvae collected in February, we are only considering the survivors. Herring larvae are susceptible to infection with both parasite types once they exceed ~15 mm in length (Rosenthal, 1967; Heath and Nicoll, 1991). This means that the larvae we investigated started accumulating parasites well before even reaching the study area. The next step to further unravel the exact link between feeding and survival should be to consider temporal differences in zooplankton composition over the lifespan of larvae as well as spatial differences along the advection route of the larvae. Furthermore, as diet of herring larvae changes as they grow (Checkley, 1982; Cohen and Lough, 1983; Munk, 1992), consideration should be given to changes in prey preference over the larval lifespan and therefore along the advection route.

The increased survival in our study area towards the end of the study period is in contrast to the continued low North Sea-wide survival (ICES, 2007; Payne *et al.*, 2009). The proportionally higher contribution from the study area to the total abundance of late stage larvae in the North Sea for this later period indicates that the differences in herring larvae survival are real and not just an artefact of the particle tracking approach or the indices used to estimate larval production. This discrepancy between temporal changes in survival locally and North Sea-wide makes it difficult to extrapolate the findings from our study area to a North Sea-wide scenario. While our results indicate that the improvement in the study area could be due to improved food intake, this does not necessarily imply that, conversely, the continued low survival in the wider North Sea is due to poor feeding conditions. However, a recent study by Payne *et al.* (2013) demonstrated lower growth rates in herring larvae in the central North Sea in years of poor (North Sea wide) survival, further supporting the link between survival and feeding conditions. A more detailed analysis of transport patterns of herring larvae and concurrent spatial variation in appropriate prey organisms and parasites could further clarify these potential links.

It is not necessarily surprising that the local survival differs from the North Sea-wide survival. The North Sea-wide survival estimate is integrated over a large and environmentally diverse area, and regional differences should be expected. Fässler *et al.* (2011) provided strong evidence of highly increased mortality in herring larvae, particularly from the Northern spawning components coinciding with the drop in overall North Sea-wide survival. As these are also the spawning components considered in this study, the two observations appear contradictory. However, Fässler *et al.* (2011) looked at mortalities in the very young larvae (<30 days). Therefore, the two studies are not directly comparable and our conclusions, at the temporal resolution of our study, are not incompatible with finer scale temporal variability in survival patterns.

Estimating survival from successive surveys of larvae is particularly difficult due to factors such as year-to-year differences in the sampling coverage. The SCAI model approach compensates for variations in timing and spatial coverage in the derivation of North Sea-wide abundance indices (Payne, 2010). However, timing and distribution of spawning has not been investigated recently, but it is assumed that the areas and times surveyed still represent the areas and times of peak larval production (ICES, 2008). The coverage of the Buchan and Orkney-Shetland spawning areas has averaged over 80% of the survey stations over the period of this study (coverage data provided by Dr Jörn Schmidt, IFM-Geomar, Germany). The only time that coverage has fallen significantly below this level was in 1996 in Orkney-Shetland, where only 49% of the stations were covered and consequently the survival index for 1996 could be either over- or underestimated.

A correlation between changes in the North Sea plankton community around 2000 and the reduction in North Sea-wide survival of herring larvae has been identified by other authors (Payne *et al.*, 2009). However, this observation by itself does not offer any explanation of how or why survival may have changed in terms of the mechanisms involved.

In this study, we provide evidence that winter survival of herring larvae in a coastal strip off the Northeast of Scotland is detectably influenced by interannual variations in cumulative food intake, as indicated by the incidence of a benign parasite acquired with the natural diet. In addition, there are suggestions of an additive detrimental effect due to digenean trematode parasites when feeding conditions are poor.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We are grateful for funding to the Marine Laboratory from the pelagic sector of the Scottish fishing industry, managed by Seafish that enabled this work to be carried out. The contributing organizations were: Scottish Pelagic Fishermen's Association, Scottish Fishermen's Federation, Shetland Fish Producers Organisation, Herring Buyers Association, Shetland Catch Ltd, and the Scottish Government Marine Directorate and Seafish. The computer simulations were carried out at the RINH/BioSS, University of Aberdeen, Beowulf linux cluster. We are very grateful to Dr Tony Travis, RINH, who made this facility available to us. Dr Ken Mackenzie provided advice on identification of parasites and on parasite ecology in general. Dr David Lusseau gave invaluable statistical help and advice. Dr Jörn Schmidt, IFM-Geomar, and Dr Norbert Rohlf at TI, Hamburg, kindly provided information and data regarding the International Herring Larvae Surveys (IHLS). We are grateful for help with zooplankton identification from Dr Steve Hay and John Fraser. Comments and suggestions from Joel Llopiz and two other anonymous reviewers were appreciated and helped improve the manuscript.

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Handling editor: Claire Paris

ICES Journal of
Marine Science

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2042–2052. doi:10.1093/icesjms/fst198

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food For Thought

Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a "critical period" driving year-class strength

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Robert, D., Murphy, H. M., Jenkins, G. P., and Fortier, L. Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a "critical period" driving year-class strength. – ICES Journal of Marine Science, 71: 2042–2052.

Received 25 June 2013; accepted 27 October 2013; advance access publication 29 December 2013.

Despite 100 years of research testing the link between prey availability during the larval stage and year-class strength, field-based evidence for Hjort's "critical period" hypothesis remains equivocal. Here, we argue that a minority of past studies have relied on sufficient taxonomical knowledge of larval fish prey preference to reveal the potential effects of variability in zooplankton prey production on larval vital rates and year-class strength. In contrast to the juvenile and adult stages, larval fish diet and prey field are often poorly resolved, resulting in the inclusion of zooplankton taxa that do not actually contribute to the diet as part of the prey field considered by fisheries scientists. Recent studies have demonstrated that when accounting for prey selectivity, the expected positive relationships between preferred prey availability and larval feeding success, growth and survival are revealed. We strongly recommend that laboratories conducting research on larval fish trophodynamics take prey selectivity into account and acquire the necessary taxonomic expertise for providing valid assessments of the influence of prey availability on larval vital rates. We make the prediction that the proportion of studies supporting the existence of a "critical period" will increase proportionally to the progress of knowledge on prey preference during the early larval stage.

Keywords: feeding success, first-feeding stage, larval trophodynamics, prey selectivity, recruitment variability, survival.

Introduction

The high variability in year-class strength of marine fish has been the focus of fisheries research since the early 20th century (Hjort, 1914). Hjort's "critical period" hypothesis predicts that "the numerical value of a year-class is determined at a very early stage, and continues in approximately the same relation to that of other year-classes throughout the life of the individuals" (Hjort, 1914, 1926). More precisely, the transition from yolk absorption to exogenous feeding is considered decisive: if first-feeding larvae fail to find adequate planktonic prey, then subsequent starvation results in high larval mortality and a reduction in year-class strength (Hjort, 1914, 1926). The "critical period" hypothesis shaped the approach to fisheries science for the following 100 years, with a large proportion of research focusing on the early life history to understand the dynamics of fish stocks. Over the past few decades, important extensions of Hjort's "critical period" hypothesis have been developed. The "match–mismatch" hypothesis (Cushing, 1972, 1990) proposed that the temporal overlap between the spring plankton bloom (prey availability) and larval production is critical for larval survival and subsequent recruitment. The "stable ocean" hypothesis (Lasker, 1978, 1981), the "optimum environmental window" hypothesis (Cury and Roy, 1989; Roy *et al.*, 1992), and the "turbulence theory" (Rothschild and Osborn, 1988; Dower *et al.*, 1997) extended the "critical period" hypothesis by incorporating hydrodynamics, in the form of windstress, upwelling, and microturbulence. These hypotheses predict that an increase in the encounter rates between larvae and their prey due to hydrodynamics results in increased foraging success and survival.

The "growth-mortality" hypothesis (Anderson, 1988) provided the first conceptual framework integrating predation, along with starvation, as a process driving larval survival and recruitment. Larval survival would directly depend on growth performance (underpinned by prey availability), in turn mediated by size- or growth-dependent predation. The "growth-mortality" hypothesis consists of three complementary mechanisms. The "bigger-is-better" hypothesis predicts that larger, faster-growing individuals are less vulnerable to predation at a given time than their smaller, slow-growing conspecifics (Shepherd and Cushing, 1980; Miller *et al.*, 1988; Leggett and Deblois, 1994). The "stage duration" hypothesis is based on the observation that larvae that grow and develop faster make an early transition to the juvenile stage, thus escaping the period of maximum mortality rate more rapidly (Chambers and Leggett, 1987; Houde, 1987). Finally, the "growth-selective predation" hypothesis predicts that the nutritional/physiological state of an individual larva may influence its probability of being captured by a predator, independent of size or developmental stage (Takasuka *et al.*, 2003; Takasuka *et al.*, 2007). The "growth-mortality" hypothesis and its three mechanisms have received broad acceptance (Govoni, 2005; Houde, 2008), with large-at-age fish larvae and fast larval growth often associated with high survival and recruitment (e.g. Hare and Cowen, 1997; Shima and Findlay, 2002; Meekan *et al.*, 2006).

Despite 100 years of research testing these multiple trophic hypotheses and mechanisms, field-based evidence for a "critical period" driving recruitment success remains equivocal (Leggett and Deblois, 1994; Houde, 2008). While some recent studies have supported the link between early larval trophodynamics and recruitment (Beaugrand *et al.*, 2003; Platt *et al.*, 2003; Castonguay *et al.*, 2008; Murphy *et al.*, 2012), several others have not observed the expected relationship (Brander, 1992; Watanabe, 2002; Agostini *et al.*, 2007; Irigoien *et al.*, 2009). In this "food for thought" contribution, we present specific examples illustrating the view that insufficient taxonomical knowledge of the actual prey field of larvae has generally precluded our ability to detect a "critical period" driving year-class strength during the early life of marine fish.

Predator–prey interactions

The dynamic relationship between predators and their prey has been the focus of extensive research by ecologists and population biologists over the past century (Berryman, 1992). The first model of trophic (predator–prey) interactions was developed by Lotka (1925) and Volterra (1931), where the attack rate of a predator was a linear function of the density of its main prey species. An important extension of this theory was the inclusion of a predator functional response, where attack rates by predators rise to a maximum (Holling, 1959). These predator–prey models have been extensively tested in terrestrial ecosystems, highlighting a high degree of diet specialization in most herbivores and predators. A classic example of diet hyperspecialization is the case of herbivorous insects, which are mostly monophagous (Hassell, 1978; Berenbaum, 1990; Jaenike, 1990). Although the selection of herbivorous insects on their static prey is an active process, selection by predators for motile prey may be partly passive and rely more on the encounter rate than on active processes (Sih and Christensen, 2001). Nevertheless, most organisms display marked prey selectivity at the species level, and knowledge of diet specificity has typically provided vital information on ecosystem function (Tegner and Levin, 1983; Messier, 1994).

The first reports of selective feeding by fish were published in the early 20th century. Scott (1920) noted that mackerel in Port Erin preyed only on a small fraction of the zooplankton assemblage. A decade later, Savage (1931) estimated prey selectivity of herring by comparing the relative abundance of prey taxa in the environment against their proportion in the guts. These studies led to Ivlev's (1961) seminal review on the trophic ecology of fish, in which he described the mechanics of prey selectivity based on 10 years of laboratory investigations. He noted that "even without taking into account cases of monophagy, when the animal consumes only one kind of food, which is especially prevalent among insects, it must be admitted that the selective faculty is, in a greater or lesser degree, to be found in all animals without exception". Two of Ivlev's most important discoveries were that selectivity for the preferred prey strengthened as its proportion increased within a given prey assemblage, but when the proportion of preferred prey within the assemblage fell below a certain threshold, and selectivity for that prey drastically declined and an alternative prey, sometimes previously selected against, became selected as the main prey (Ivlev, 1961). These results confirmed that prey selectivity is a mechanism allowing predators to optimize energy gained over energy spent, independent of the quality of the available prey field. Since the publication of Ivlev's seminal work, species-specific diet and prey selectivity during the juvenile (e.g. Juanes and Conover, 1995; Arrhenius, 1996) and adult (e.g. Cabral and Murta, 2002; Darbyson *et al.*, 2003) stages of fish were extensively described through the analysis of gut content and stable isotopes. This information is commonly taken into account in mass-balance modelling (e.g. Bundy, 2005).

In contrast to the juvenile and adult stages, larval fish diet is often poorly resolved, and taxonomical resolution tends to decrease from late larvae to first-feeding larvae. In a review of larval fish feeding ecology, Llopiz (2013) summarized 204 investigations (taxon–article combinations), among which 106 (52%) investigations provided a full assessment of diet composition. A detailed review of these 106 diet composition investigations revealed that prey of first-feeding larvae were identified to the species or genus levels in only 21 cases (10% of all feeding investigations). In all other instances, prey of first-feeding larvae were classified to the subclass level (e.g. copepod nauplii) or, at best, to the order level (e.g. calanoid nauplii). Another recent review on larval fish foraging ecology only focused on selectivity for prey types without any mention of potential selection at the species or genus levels, reflecting the general absence of information on the scale at which prey selectivity operates (Nunn *et al.*, 2012). This lack of focus on the taxonomical resolution of larval fish trophodynamics likely stems from the quasi-impossibility of observing larval fish foraging in their natural environment, combined with the difficulty of identifying the small mesozooplankton prey found in the stomachs of individuals captured at sea. These inherent challenges in larval diet characterization may explain why several authors have considered all zooplankton organisms that are smaller than the larval gape aperture as potential prey (Pepin and Penney, 1997; Rowlands *et al.*, 2008; Morote *et al.*, 2010; Bernal *et al.*, 2013). Although size is likely an important driver of prey preference, assuming that all zooplankton organisms in a given size range are of similar importance to fish larvae will systematically result in the consideration of taxa that are selected against and do not significantly contribute to the diet.

Larval fish trophodynamics

The feeding ecology of larval fish has been studied extensively as a means of investigating the link between larval survival and recruitment. Llopiz (2013) discussed the existence of distinct general patterns in larval feeding ecology across latitudes and taxa. At high latitudes, calanoid copepods generally constitute the most important prey types, with a shift from smaller to larger prey through larval ontogeny (Llopiz, 2013). Species from lower latitudes tend to feed on more diverse prey taxa, but are also characterized by narrower niche breadth and do not generally exhibit ontogenetic diet shifts (Llopiz, 2013). Beyond these general spatial patterns, some recent studies have investigated how diet composition and prey selectivity may vary seasonally and interannually within a given population (Dickmann *et al.*, 2007; Robert *et al.*, 2008; Llopiz and Cowen, 2009; Young *et al.*, 2010; Murphy *et al.*, 2012). Prey preference and diet composition remained generally constant across seasons for larval taxa in lower latitudes (Llopiz and Cowen, 2009), whereas strong seasonal variations were reported at higher latitudes as a result of changing zooplankton prey field (e.g. Dickmann *et al.*, 2007). Interestingly, the niche breadth of some larval fish taxa was also shown to vary interannually, with a sharp increase under conditions of low preferred prey availability (Young *et al.*, 2010; Murphy *et al.*, 2012); however, even when densities of preferred prey availability were low, larvae still preyed selectively and were not foraging on all taxa found in their environment (Young *et al.*, 2010; Murphy *et al.*, 2012). The remarkable diversity in the feeding ecologies of larval fish, evident even among co-occurring taxa, highlights the need to resolve diet composition at the species level, as general patterns in larval trophodynamics are not likely to provide us with insights on how fluctuations in the zooplankton assemblage may affect larval vital rates and recruitment.

Studies that have considered both larval gut contents and prey availability with a high taxonomical resolution (i.e. species or genus level) have generally confirmed that first-feeding larvae, much like the juveniles and adults, show strong preference for specific prey taxa (Llopiz and Cowen, 2008; Robert *et al.*, 2008; Voss *et al.*, 2009). Selection for a given type of prey is driven by the ratio of energy gained over energy expended for its capture. For example, cyclopoid copepod nauplii are frequently selected against, which may be due to their lower activity level compared with calanoid copepods (Buskey *et al.*, 1993), whereas the red pigmentation of cladocerans may increase their visibility and selectivity compared with prey of similar size (Wong *et al.*, 2008). And while selection for specific prey types may be a passive process that reflects a prey type's high abundance and behaviour (Kristiansen *et al.*, 2009), passive selection may evolve into an active process later in the larval stage (Rowlands *et al.*, 2008). Based on a table compiled by Robert *et al.* (2008), to which were added subsequent studies (period 2008–2013; Table 1), the proportion of prey selectivity studies (i.e. diet composition contrasted to the relative abundance of potential prey in the field) that have considered the diet of first-feeding larvae with high taxonomical resolution was 49% (18 of 37 studies). All these 18 studies concluded that strong prey selectivity occurred at the species (or genus) level, which strongly suggests that a match between larvae and specific prey items is important for larval survival (Llopiz and Cowen, 2008; Robert *et al.*, 2008; Murphy *et al.*, 2012).

High availability of preferred prey, identified through the initial assessment of prey preference, has been linked to high feeding success and growth during the early larval stage (e.g. Buckley and Durbin, 2006; Robert *et al.*, 2009; Sponaugle *et al.*, 2009; Leclerc *et al.*, 2011). Large-at-age larvae are thought to be better swimmers and foragers that would experience a relatively high survival rate due to their lower vulnerability to predation and greater ability to capture prey (e.g. bigger-is-better); however, few studies have tested the link between feeding success and otolith-derived growth in individual wild-caught larvae to test this paradigm (but see Dower *et al.*, 2009; Robert *et al.*, 2014). These few tests nevertheless confirmed the prediction that large-at-age larvae were characterized by a larger volume of prey in their stomachs relative to smaller-at-age individuals (Dower *et al.*, 2009; Robert *et al.*, 2014). A positive link has also been found between growth rates and the availability of preferred planktonic prey (Robert *et al.*, 2009; Sponaugle *et al.*, 2010; Murphy *et al.*, 2013), which points to the critical importance of specific prey taxa as drivers of survival. These recent findings that link larval trophodynamics, growth, and survival in a diverse set of larval fish taxa highlight the importance of relying on highly resolved larval prey preference during the first-feeding stage to assess processes underlying recruitment dynamics.

Evidence for a critical period

Historically, the majority of studies looking into the existence of a "critical period" during the first-feeding stage of fish have been conducted in the North Atlantic, in some of the same systems contemplated by Johan Hjort when developing his seminal hypothesis. Although this focus on the North Atlantic explains in part why most of the support for a "critical period" comes from high latitude ecosystems, the relatively low biodiversity of high latitude foodwebs has likely played a role in revealing links between feeding conditions and larval vital rates. North Atlantic zooplankton assemblages are only composed of a few highly abundant taxa, making it easier to identify key prey species, especially when such prey taxa dominate the zooplankton assemblage by numbers and/or biomass. A classic example is the obvious trophic link between the dominant calanoid copepod *Calanus finmarchicus* and early life stages of some Atlantic cod stocks in the Northeast Atlantic (Ellertsen *et al.*, 1989; Sundby and Fossum, 1990; Beaugrand *et al.*, 2003).

Atlantic cod *Gadus morhua* is by far the marine fish species that has received the most attention over the past century. Over 40 studies have described the diet of its larvae and juveniles. A synthesis of this work has revealed that cod larvae in stocks located in the northern portion of the species' latitudinal range depend heavily upon the nauplius stages of the large calanoid copepod *C. finmarchicus*, whereas larvae from stocks located in the southern portion of the range primarily rely on nauplius stages of the medium-sized calanoid copepod *Pseudocalanus* spp. (Heath and Lough, 2007). The current knowledge of larval cod diet and prey selectivity supports the Ivlev function previously reported by Ellertsen *et al.* (1989) between *Calanus* sp. nauplii density and feeding success and allowed Buckley and Durbin (2006) to reveal a strong link between growth rate and preferred prey availability. A strong relationship has also been reported between year-class strength and preferred zooplankton prey abundance in the North Sea (Beaugrand *et al.*, 2003), highlighting the existence of a critical period for that cod stock.

Another system where detailed knowledge of diet revealed functional relationships between prey availability and larval vital rates is the Atlantic mackerel *Scomber scombrus* in the southern Gulf of St Lawrence. Three independent studies have described larval diet and prey selectivity at a high taxonomical resolution (Ringuette *et al.*, 2002; Robert *et al.*, 2008; Paradis *et al.*, 2012),

Table 1. Summary of the literature on larval prey selectivity during the first-feeding and late larval stages.

Family	Species	Region	Preferred prey		Reference
			First-feeding stage	Late larval stage	
Ammodytidae					
	Ammodytes americanus	Long Island Sound	*Temora longicornis* N	*Temora longicornis* C	**Monteleone and Peterson (1986)**
	Ammodytes marinus	Northern North Sea	Calanoid N	Calanoid N	Economou (1991)
	Ammodytes sp.	Gulf of St Lawrence	*Calanus finmarchicus* E	*Calanus finmarchicus* E and N	**Demontigny *et al.* (2012)**
Callionymidae					
	Callionymus lyra	Western English Channel	Copepod N	*Calanus helgolandicus* C	Fortier and Harris (1989)
	Not defined	Offshore western Australia	–	Cyclopoid C, *Euterpina acutifrons* C	Sampey *et al.* (2007)
Carangidae					
	Trachurus declivis	Tasman Sea	Copepod N	*Microsatella rosea* C	Young and Davis (1992)
Clupeidae					
	Clupea harengus	Blackwater Estuary	*Acartia* C	*Acartia* C	**Fox *et al.* (1999)**
		Newfoundland	Calanoid N, cyclopoid N, bivalve larvae	Calanoid N, cyclopoid N, bivalve larvae	Pepin and Penney (1997)
	Ethmidium maculatum	Central Chile	Copepod E	Copepod E and C	Llanos-Rivera *et al.* (2004)
	Sardina pilchardus	North Sea	*Pseudocalanus* spp., *Paracalanus* spp., *Calanus* spp.	No selection	**Voss *et al.* (2009)**
	Sardina pilchardus	Western Mediterranean	*Cadonellopis* sp., Copepod N	Calanoid N	Morote *et al.* (2010)
	Sardinops sagax	Central Chile	Mollusk larvae	Copepod C	Llanos-Rivera *et al.* (2004)
	Sprattus sprattus	Baltic Sea	Copepod N	*Acartia* C	Voss *et al.* (2003)
		Baltic Sea	*Acartia* N, *Centropages hamatus* N, *Temora longicornis* N	*Acartia* C, *Centropages hamatus* C	**Dickmann *et al.* (2007)**
		Western English Channel	Copepod N	*Paracalanus parvus* C	Fortier and Harris (1989)
		North Sea	*Pseudocalanus* spp., *Paracalanus* spp., *Calanus* spp.	*Acartia* spp., *T. longicornis*, *Pseudo-*/*Paracalanus* A	**Voss *et al.* (2009)**
	Strangomera bentincki	Central Chile	Copepod E and N	Copepod E and C	Llanos-Rivera *et al.* (2004)
Cynoglossidae					
	Cynoglossus spp.	Offshore western Australia	–	Cyclopoid C	Sampey *et al.* (2007)
Engraulidae					
	Engraulis anchoita	Argentine Sea	Small copepod N	–	Viñas and Ramírez (1996)
	Engraulis encrasicolus	Northwest Adriatic Sea	Calanoid and cyclopoid N	–	Conway *et al.* (1998)
	Engraulis encrasicolus	Western Mediterranean	Copepod N	*Evadne*	Morote *et al.* (2010)
	Engraulis encrasicolus	Adriatic Sea	–	*Oncea* spp., *Euterpina acutifrons*, *Microstella* spp.	Borme *et al.* (2009)
	Engraulis ringens	Central Chile	Copepod E and N	Copepod E and C	Llanos-Rivera *et al.* (2004)
Gadidae					
	Boreogadus saida	Northeast Water Polynya	Copepod N	–	Michaud *et al.* (1996)
	Gadus morhua	Southerly populations	*Pseudocalanus* N	*Pseudocalanus* C, *Paracalanus* C	**Heath and Lough (2007)** and references therein
		Northerly populations	*Calanus* N	*Calanus finmarchicus* C	**Heath and Lough (2007)** and references therein

Continued

Table 1. *Continued*

Family	Species	Region	Preferred prey		Reference
			First-feeding stage	Late larval stage	
		Magdalen shallows	*Pseudocalanus* spp. N	*Pseudocalanus* spp. C	**Robert *et al.* (2011)**
	Melanogrammus aeglefinus	Northern North Sea	Calanoid N, *Calanus* eggs	*Pseudocalanus elongatus* C, *Temora longicornis* C, Evadne sp., Euphausiids	Economou (1991)
		Irish Sea	Copepod N	–	Rowlands *et al.* (2008)
		Georges Bank	Copepod E, medium-sized calanoid N	*Pseudocalanus minutus* C	Kane (1984)
	Merlangius merlangus	Northern North Sea	Calanoid N	*Pseudocalanus elongatus* C, *Acartia clausii* C, *Calanus finmarchicus* C	Economou (1991)
		Irish Sea	Copepod N	–	Rowlands *et al.* (2008)
		Western English Channel	Copepod N	Copepod N, *Pseudocalanus elongatus* C	Fortier and Harris (1989)
	Pollachius virens	Northern North Sea	Calanoid N	*Calanus finmarchicus* C, *Acartia clausii* C, *Oithona* C	Economou (1991)
	Theragra chalcogramma	Bering Sea	*Metridia* N, *Microcalanus* N		**Hillgruber *et al.* (1995)**
	Trisopterus esmarkii	Northern North Sea	Calanoid N, *Calanus* eggs	*Pseudocalanus elongatus* C, *Calanus finmarchicus* C	Economou (1991)
Gobiidae					
	Not defined	Offshore western Australia	–	*Bestiolina similis* C, *Oithona* C	Sampey *et al.* (2007)
Istiophoridae					
	Istiophorus platypterus	Straits of Florida	*Farranula* C *Evadne*	*Farranula* C, *Evadne*, fish larvae	**Llopiz and Cowen (2008)**
	Makaira nigricans	Straits of Florida	*Farranula* C *Evadne*	*Farranula* C, *Evadne*, fish larvae	**Llopiz and Cowen (2008)**
Labridae					
	Tautogolabrus adspersus	Newfoundland	Calanoid N, cladocerans	Calanoid N, cladocerans	Pepin and Penney (1997)
	Thalassoma bifasciatum	Straits of Florida	No early stage larvae	*Farranula* C, *Oncaea* C, harpacticoids	Sponaugle *et al.* (2009)
Leiognathidae					
	Not defined	Offshore western Australia	–	*Oithona attenuata* C, calanoid N and C	Sampey *et al.* (2007)
Liparidae					
	Liparis sp.	Newfoundland	Calanoid N, euphausids	Calanoid N, euphausids	Pepin and Penney (1997)
Merlucciidae					
	Merluccius merluccius	Northwestern Mediterranean	*Clausocalanus* spp.	*Clausocalanus* spp.	**Morote *et al.* (2011)**
Monacanthidae					
	Not defined	Offshore western Australia	–	Polychaetes	Sampey *et al.* (2007)

Myctophidae				
Lampanyctus pusillus	Western Mediterranean	Copepod N, Oncaeid N	*Clausocalanus* spp. C, Larvaceans	Bernal *et al.* (2013)
Osmeridae				
Mallotus villosus	Newfoundland	Cyclopoid N, calanoid C	Cyclopoid N, calanoid C	Pepin and Penney (1997)
Pinguipedidae				
Not defined	Offshore western Australia	–	*Temora* C, *Bestiolina similis* C, cyclopoid C, decapod larvae	Sampey *et al.* (2007)
Pleuronectidae				
Glyptocephalus cynoglossus	Newfoundland	Calanoid N and C, bivalve larvae, cladocerans	Calanoid N and C, bivalve larvae, cladocerans	Pepin and Penney (1997)
Hippoglossoides platessoides	Northern North Sea	Calanoid N	*Calanus finmarchicus* C	Economou (1991)
	Newfoundland	Calanoid N and C	Calanoid N and C	Pepin and Penney (1997)
Pleuronectes americanus	Newfoundland	Bivalve larvae, cladocerans	Bivalve larvae, cladocerans	Pepin and Penney (1997)
Pleuronectes ferrugineus	Newfoundland	Calanoid N, cladocerans	Calanoid N, cladocerans	Pepin and Penney (1997)
Sciaenidae				
Leiostomus xanthurus	Northern Gulf of Mexico	*Oncaea* C	*Paracalanus* C, *Oncaea* C	**Govoni *et al.* (1986)**
Micropogonias undulatus	Northern Gulf of Mexico	*Oncaea* C, *Oithona* C, *Acartia tonsa* C	*Paracalanus* C	**Govoni *et al.* (1986)**
Scophthalmidae				
Phrynorhombus norvegicus	Western English Channel	Copepod N	*Acartia* C, *Oithona* C	Fortier and Harris (1989)
Scombridae				
Auxis spp.	Straits of Florida	Appendicularians	Appendicularians	Llopiz *et al.* (2010)
Euthynnus alletteratus	Straits of Florida	Appendicularians	Appendicularians, fish larvae	Llopiz *et al.* (2010)
Katsuwonus pelamis	Eastern Indian Ocean	Appendicularians	Appendicularians	Young and Davis (1990)
	Straits of Florida	Appendicularians	Appendicularians, fish larvae	Llopiz *et al.* (2010)
Scomber scombrus	Long Island Sound	*Temora longicornis* N, *Pseudocalanus* N	–	**Peterson and Ausubel (1984)**
	Magdalen Shallows	*Pseudocalanus* N, *Temora* N	Cladocerans, fish larvae	**Robert *et al.* (2008)**
	Gulf of St Lawrence	*Oithona* spp. N, *Temora longicornis* N	*Oithona* spp. N, *Temora longicornis* N	**Paradis *et al.* (2012)**
	Scotian Self	Copepod N	Fish larvae	Fortier and Villeneuve (1996)
Scomberomorus spp.	Coral Sea	Fish larvae	Fish larvae	Jenkins *et al.* (1984)
Thunnus alalunga	Eastern Indian Ocean	Copepod N, corycaeid C	Copepod N, corycaeid C	Young and Davis (1990)
Thunnus maccoyi	Eastern Indian Ocean	Copepod N, corycaeid C	Corycaeid C	Young and Davis (1990)
Thunnus thynnus	Mediterranean	Copepod N	Cladocerans	Catalan *et al.* (2011)
Thunnus spp.	Straits of Florida	Calanoid N and C, appendicularians, *Evadne* spp., *Farranula* N and C, fish larvae	Calanoid N and C, appendicularians, *Evadne* spp., *Farranula* N and C, fish larvae	**Llopiz *et al.* (2010)**
Sebastidae				
Sebastes spp.	Flemish Cap	*Calanus* E and N	*Calanus* E and N, cyclopoid C	**Anderson (1994)**
	Northern Gulf of St Lawrence	*Calanus* E	*Calanus* E	**Runge and de Lafontaine (1996)**
Soleidae				
Microchirus variegatus	Western English Channel	Copepod N	*Temora longicornis* C, *Evadne*, Polychaete larvae	Fortier and Harris (1989)

Continued

Table 1. *Continued*

Family	Species	Region	Preferred prey First-feeding stage	 Late larval stage	Reference
Sparidae					
	Chrysophrys auratus	Port Phillip Bay	*Paracalanus* spp. N, *Acartia* spp. N, *Calanus* spp. N	*Paracalanus* spp. C, Cladocerans (*Podon, Evadne, Penilia*)	**Murphy *et al.* (2012)**
Stichaeidae					
	Lumpenus lampretaeformis	Gulf of St Lawrence	*Calanus* sp. N		**Demontigny *et al.* (2012)**
	Stichaeus punctatus	Newfoundland	Calanoid N and C, cyclopoid C, euphausids	Calanoid N and C, cyclopoid C, euphausids	Pepin and Penney (1997)
	Stichaeus punctatus	Gulf of St Lawrence	*Calanus* sp. N	*Calanus* sp. N	**Demontigny *et al.* (2012)**
	Ulvaria subbifurcata	Newfoundland	Calanoid N, cladocerans	Calanoid N, cladocerans	Pepin and Penney (1997)

No stage differentiation was made for species described by Pepin and Penney (1997) as prey selectivity was integrated over entire larval life. E, N, and C represent copepod eggs, nauplii, and copepodites, respectively. References indicated in bold characters represent studies where prey selectivity was determined at the species or genus level during the first-feeding stage. Table modified from Robert *et al.* (2008), with the addition of literature published during the period 2008–2013.

and these studies concluded that key prey taxa for first-feeding mackerel larvae are the nauplius stages of the calanoid copepods *C. finmarchicus*, *Pseudocalanus* spp., and *Temora longicornis*. Interestingly, Paradis *et al.* (2012) reported that during 2 years of low preferred prey density, mackerel larvae selected for the nauplius stages of *Oithona similis*, a small cyclopoid copepod usually selected against. In agreement to Ivlev's findings (Ivlev, 1961), they concluded that while larvae demonstrated flexibility in feeding behaviour in response to fluctuations in the abundance of their preferred prey, the alternative prey did not provide an optimal balance of energy gained over energy expended, which resulted in poor survival rates. Furthermore, both feeding success and growth were linked to the availability of preferred prey during the first-feeding stage of Atlantic mackerel (Robert *et al.*, 2009). Evidence of a critical period was found in this species, with a strong relationship linking year-class strength to the production of preferred copepod prey during the first-feeding period, by using a multiannual time-series of zooplankton sampled during the season of larval emergence (Castonguay *et al.*, 2008).

In Australian snapper *Chrysophrys auratus*, a 7-year time-series of larval abundance combined with a 5-year time-series of zooplankton biomass were vital in elucidating links among prey availability, larval growth, and recruitment. First-feeding snapper strongly selected for *Paracalanus* sp. and *Acartia* sp. nauplii (Murphy *et al.*, 2012, 2013), and years characterized by lower preferred prey availability during the first-feeding stage were characterized by slower larval growth and lower recruitment of 0-age individuals (Murphy *et al.*, 2013), compared with years with high preferred prey availability. Similar to cod and mackerel, this critical period in the early life of snapper could only be revealed following the detailed assessment of diet composition and prey selectivity during the first-feeding stage.

Decadal time-series of year-class strength, larval vital rates and taxonomically resolved zooplankton abundance, however, remain scarce, explaining the small number of studies providing a direct test to the "critical period" hypothesis. Among published tests based on zooplankton abundance, studies considering bulk zooplankton as the potential larval prey field generally failed in revealing the expected positive relationship between prey abundance and recruitment (e.g. Agostini *et al.*, 2007; Irigoien *et al.*, 2009), whereas those providing evidence for a critical period systematically relied on taxonomically resolved zooplankton data and focused on specific taxa based on the prior assessment of prey selectivity (Beaugrand *et al.*, 2003; Castonguay *et al.*, 2008; Murphy *et al.*, 2012). These contrasting results support the importance of acquiring detailed taxonomical knowledge of prey preference and diet composition before attempting to relate year-class strength of a fish stock to inter-annual variability in prey availability during the larval stage.

Future research perspectives

Because larval fish do not prey randomly on the suite of potential prey taxa co-occurring in the plankton, future tests of the "critical period" or any other trophic hypothesis should rely on the prior detailed assessment of diet composition and prey selectivity. The relative importance of the different potential prey taxa in fulfilling energy requirements of larval fish can only be resolved through the study of larvae captured at sea. Laboratory-based feeding experiments, although useful for determining vital characteristics such as maximum feeding ration and point of no return, generally use artificial prey fields (typically rotifers and/or *Artemia* sp.) that are not typical of those encountered by larvae in the wild. Even in cases where natural zooplankton assemblages are used (e.g. Houde, 1975; Stepien, 1976), it remains an extraordinary challenge to adequately reproduce the dynamic foraging environment of larval fish, made up of predators, prey patchiness, and complex physical processes.

To develop a reliable plankton index to help forecast year-class strength, an annual field survey would ideally cover a representative portion of spawning grounds for the stock at time of larval emergence (early larval stage) and the zooplankton assemblage should be sampled using fine mesh (e.g. 50 μm), providing an absolute abundance estimate of the tiny organisms (e.g. copepod nauplii, protozoans) most likely contributing to the prey field of first-feeding larvae. Quantitative estimation of the small fraction of the mesozooplankton assemblage is critical to identifying preferred prey through analysis of prey selectivity. These data are also essential for assessing the role of interannual variability in preferred prey availability on year-class strength, and ultimately, for developing a plankton index for recruitment prediction.

Field-based research, however, bears its own challenges, such as the difficulty to detect soft-bodied organisms in larval fish guts. In particular, recent studies suggested an important role of protozoans during the first-feeding stage of larval fish species characterized by a straight gut (e.g. Pepin and Dower, 2007; Montagnes *et al*., 2010). Several protozoans such as naked ciliates are digested almost instantly, making them difficult to quantify through visual examination. This problem could be partly resolved by molecular detection (e.g. Craig *et al*., 2013), which would help in characterizing the role of these organisms in larval diet. Another important challenge is the difficulty in sampling the zooplankton prey field on a scale that compares with that of a larva's ambit (Dower *et al*., 2002). This technical limitation makes it nearly impossible to assess variability in prey availability at the individual level. Some past studies have attempted sampling the zooplankton assemblage at fine scales that better reflected variability in prey supply perceived by individual larvae (e.g. Houde and Alpern Lovdal, 1985; Taggart and Leggett, 1987), but they have generally failed to reveal a link between prey availability and vital rates. On the other hand, none of those studies have examined prey selectivity at a high taxonomical resolution. We argue that without critical information on larval prey preference, any existing relationship between vital rates and prey availability will remain concealed by the bulk of zooplankton organisms that do not contribute to larval diet in a significant way.

Even when the small fraction of mesozooplankton is quantitatively sampled, an additional problem may lie in the lack of expertise for identifying these assemblages at a sufficient taxonomical resolution to allow for a species-specific assessment of prey preference. We thus encourage laboratories conducting research on the trophodynamics of larval fish to acquire the taxonomic expertise that will allow them to conduct sound assessments of the influence of prey availability on larval vital rates. Finally, as Houde (2008) recently stated, the most important challenge ahead for fisheries scientists is to achieve and maintain decadal time-series of year-class strength, larval abundance and dynamics, and abundances of larval preferred prey. We contend that such time-series, based on relevant sampling scales for larvae and their preferred prey, constitute the baseline for future investigation on recruitment variability, without which further tests of trophic hypotheses will remain futile.

Conclusion

In his recent review on the advancements of recruitment research during the past century, Houde (2008) noted that "tests of the Critical Period hypothesis once became an obsession, although support for it was inconsistent and equivocal". We argue that only a minority of those past studies have relied on sufficient taxonomical knowledge of the actual prey field of fish larvae to allow detecting the potential effects of variability in zooplankton prey production on larval vital rates and year-class strength. Recent studies have demonstrated that when focusing on preferred prey, the expected positive relationships between prey availability and larval feeding success, growth, and survival are revealed. We make the prediction that the proportion of studies supporting the existence of a "critical period" will increase proportionally to the progress of taxonomical knowledge on prey preference during the early larval stage. Information on diet composition for a given population/species will also feed into individual-based modelling to help predict the larval survival rate and year-class strength from diverse scenarios of seasonal production of preferred prey.

Acknowledgements

We thank A. Takasuka as well as 3 anonymous referees for providing constructive comments that improved an earlier version of this manuscript.

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Handling Editor: Howard Browman

ICES Journal of
Marine Science

ICES
International Council for
the Exploration of the Sea
CIEM
Conseil International pour
l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2053–2063. doi:10.1093/icesjms/fsu030

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Making use of Johan Hjort's "unknown" legacy: reconstruction of a 150-year coastal time-series on northeast Arctic cod (*Gadus morhua*) liver data reveals long-term trends in energy allocation patterns

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Kjesbu, O. S., Opdal, A. F., Korsbrekke, K., Devine, J. A., and SkjæraasenJon Egil Making use of Johan Hjort's "unknown" legacy: reconstruction of a 150-year coastal time-series on northeast Arctic cod (*Gadus morhua*) liver data reveals long-term trends in energy allocation patterns – ICES Journal of Marine Science, 71: 2053–2063

Received 1 July 2013; accepted 2 February 2014; advance access publication 11 March 2014.

Hidden within the seminal 1914 publication by Johan Hjort, we find what is probably one of the first comprehensive teleost time-series ever published. The series is liver size and fat content of northeast Arctic (NEA) cod measured during the traditional winter fishery in Lofoten, Northern Norway, in 1880–1912 and 1883–1913, respectively. The data were collected well before the advent of the great industrialized fisheries in the 1930s. The raw data used by Hjort originate from annual reports of the Lofoten fishery, initiated by Member of Parliament and pioneer fishery inspector of Northern Norway, Ketil Motzfeldt, in 1859. Based on these reports and following various calibration exercises, we present robust estimates of the hepatosomatic index (HSI) from 1859 to 2012 (except 1863), i.e. over 153 years—extending Hjort's analysis both backwards (1859–1879) and forwards (1913–present). This series of bulk HSI contained five major periods: 1859–1880, 1881–1919, 1920–1974, 1975–2003, and 2004–2012; the highest HSI was recorded 1920–1974, whereas the lowest was from the most recent period. Despite variability, total length was a significant predictor of HSI, 1932–2012. A weak but significant relationship existed with both total-stock biomass and ocean temperature, as well as with the North Atlantic Oscillation winter index under a 1-year lag. The present exceptionally long HSI series will give an excellent opportunity for further research on the "quality of the cod" in a historic perspective.

Keywords: Atlantic cod, hepatosomatic index, Johan Hjort, NAO, temperature, time-series.

Introduction

The importance of Johan Hjort's pioneering efforts for the development of marine biology generally and fisheries biology especially can hardly be overstated (Sinclair, 1997; Houde, 2008). Today, his main legacy includes "the critical period hypothesis" for first-feeding larvae, drift (advection) of early life stages including mortality, the formation of strong and weak year classes, spawning migration routes, and finally, stock variability linked to ecological conditions. His main species of interest were Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*). Above all, his seminal book "Fluctuations in the Great Fisheries of Northern Europe Viewed in the Light of Biological Research" (Hjort, 1914) stimulated research all over the world and remains integral to modern fisheries management, i.e. this ICES volume is still frequently cited 100 years after its release.

Perhaps less known is the fact that Hjort showed one of the first, if not the first, comprehensive time-series on a marine fish with his presentation of data on commercial liver landings of northeast Arctic (NEA) cod from the Lofoten area, the largest coastal fishery in Norway, in the period from 1880 to 1912. The corresponding fat content was also reported for the years 1883–1913. These efforts should not be considered an original approach, since several of his contemporaries were completing similar studies of annual variations in biological traits, e.g. the fat content in Atlantic herring and European sprat (*Sprattus sprattus*; see figures and references in Hjort, 1914). What was novel was the markedly longer length of his established time-series compared with others that existed in this period and that he placed his findings within the context of population dynamics. However, Helland-Hansen and Nansen (1909) were apparently the first to put up an ecological framework by relating "physical conditions" (ocean temperature) with "biological conditions", here studying a limited subset (1899–1906) of the same liver (and roe) data as used by Hjort (1914). Today, time-series analyses are essential in a broad range of monitoring programmes and analytic assessments, but also to disentangle and show complex causal links, like that of climate (e.g. Ottersen *et al.*, 2010; Petitgas *et al.*, 2013) and fisheries-induced evolution (e.g. Rijnsdorp, 1993; Heino and Godø, 2002) on teleost traits.

Several studies on the monthly resolved Russian NEA cod liver data (1927–present) from the Barents Sea (Sandeman *et al.*, 2008; Yaragina, 1996, 2010), as well as other related studies, including experimental (Skjæraasen *et al.*, 2009), have provided a large amount of knowledge of factors affecting this stock's investment in liver energy storage. In particular, the close link between relative liver size (hepatosomatic index; HSI) and liver energy content (Lambert and Dutil, 1997; Skjæraasen *et al.*, 2010), but also with the abundance of the main prey, Barents Sea capelin (*Mallotus villosus*), as well as environmental temperature (Sandeman *et al.*, 2008) stand out as important (Marshall *et al.*, 1998). However, as the earlier part of the Barents Sea liver data (1927–1966) is incomplete or grouped by fish weight instead of length, Sandeman *et al.* (2008) restricted their statistical analyses from 1967 onwards.

Hjort was mainly motivated by the importance of the liver as a commercial product in its own right, but also by the association between liver size and "the quality of the cod", or more specifically, "its condition in point of nourishment" (*sic*) (Hjort, 1914). Condition is here analogous with "the percentage in volume of the oil". The main finding was, in his own words, "the remarkable cyclicity of liver landings", which was accompanied by a similar co-variation in liver fat content (Figure 1). In this article, we revisit Hjort's original time-series and supplement his data with both newer and older data on liver landings (Figure 2). The existence of older, similar data (1859–1879) was somewhat unexpected because there is no specific mention of them in Hjort (1914). The primary source of data was the yearly reports and catch statistical time-series from the Lofoten fisheries (e.g. the Official Fisheries Statistics). Their origin can be traced back to the onset of a government initiated regulation of fisheries in Northern Norway, passed as an amendment to the existing Law of Lofoten (from 1816) in 1858. The intent of the amendment was to shift regulatory power from private proprietors to federal authorities. A significant political advocate for the making and passing of this amendment was Member of Parliament, Ketil Motzfeldt, who, in the following year, became the first Fishery Inspector of Northern Norway and initiated what would become the regular status report series of the Lofoten fisheries, although named differently over time (Anon, 1859–2012). Hence, Hjort could access annual and seasonal information from "the Fisheries Inspectors telegraph" on the "average quantity" of "skrei" and the corresponding amount of liver (and occasionally roe; Hjort, 1914). "Skrei" is from old Norse and means to move or to travel, cf. the long spawning migration route of NEA cod from the Barents Sea to the Norwegian coast. The report series, including catch statistics, was primarily intended as a bookkeeping system for social costs and services, as well as, for example, commercially relevant parameters such as weekly turnover, landings, production, and bait prices. In its original form, the reports included no account of biological or ecological aspects. Its biological negligence is exemplified by the common gauge for "quality" being the number of cod required to fill a barrel with the liver. Naturally, Hjort was bound to the same coarse metrics as applied there, i.e. bulk volumetric landings of the liver (initially number of 116 l barrels and later hectolitres), and total number of landed cod (Figure 2). Since Hjort (1914) also contains records of body weights, the "bulk HSI", a term used by us, could be estimated.

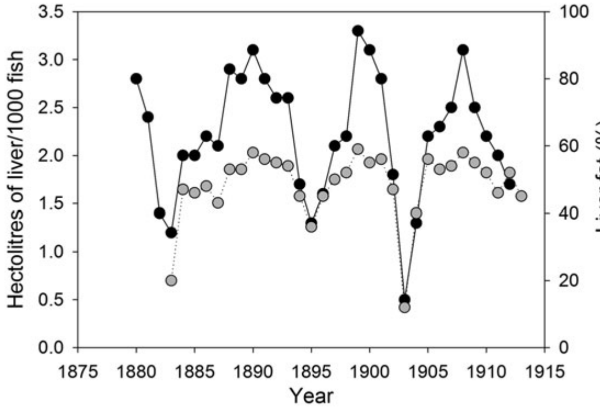

Figure 1. Redrawn plot of Hjort's Figure 107 (Hjort, 1914) showing hectolitres of liver per thousand fish (dark circles) and the corresponding liver fat content (grey circles) for northeast Arctic cod in the Lofoten fishery, 1880–1912 and 1883–1913, respectively.

The primary task of our work was to expand as far as possible Hjort's liver data both backwards and forwards in time in a coherent way to obtain (i) a better insight into the "condition" of NEA cod at the time of his seminal research, and (ii) a long-term proxy of the dynamics of liver size and thereby energy allocation patterns in this stock. In the analysis, we opted for HSI as the universal expression of investment in liver size vs. body size. We consulted recent publications on the relationship between fat content and HSI, as well as fisheries-independent annual values on the mean HSI, to ground-truth as much as possible the present series on bulk HSI. Finally, we examined the whole time-series in terms of general trends and shorter oscillations, concentrating on investigations into broad mechanisms that might be responsible for the observed patterns in HSI.

Material and methods

General overview

Commercial landings

Commercial landings of NEA cod were restricted to be from within the same geographical area during the spawning season, i.e. the Lofoten area. This defines the main spawning time and ground of this major gadoid stock. Immature fish and fish that skip spawning were unaccounted for because they rarely undertake such migrations to the Norwegian coast and therefore remain in the Barents Sea feeding area (Trout, 1957; Jørgensen *et al.*, 2006; Yaragina, 2010; Skjæraasen

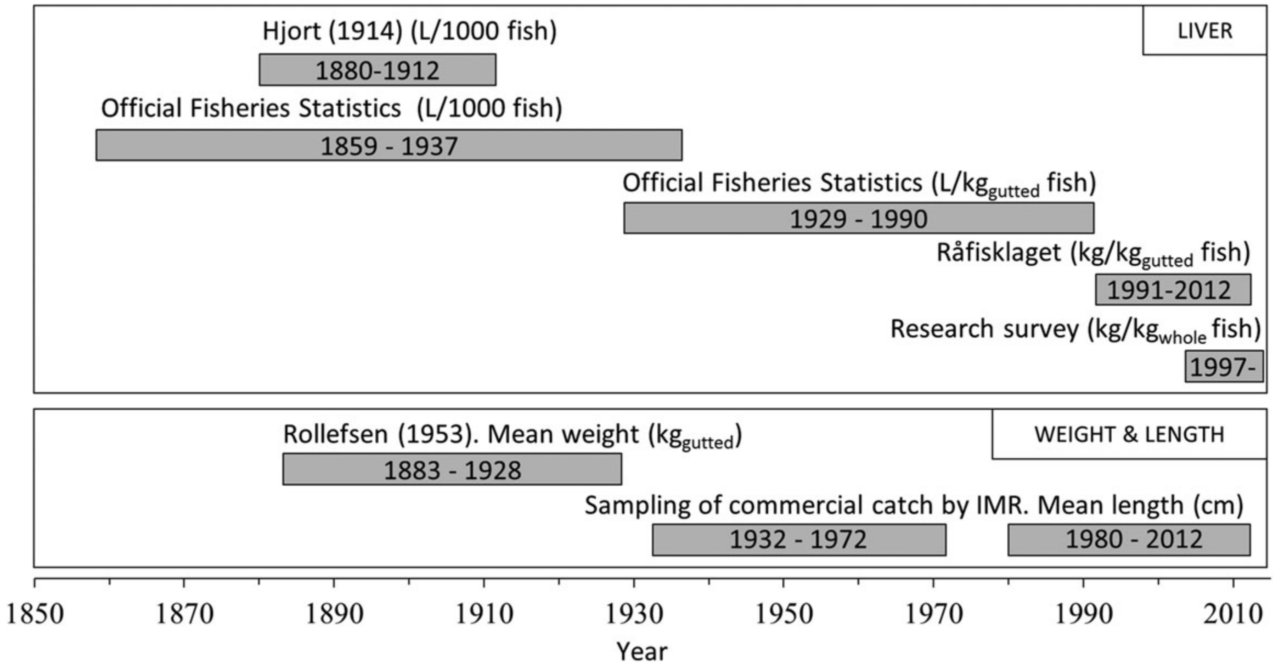

Figure 2. Overview of data sources from the annual Lofoten cod fishery and research monitoring programme. Upper panel shows Fisheries Statistics data of the relative amount of liver, including the data consulted by Hjort (1914), presented either in litre of liver per thousand fish or litre of liver per kilo gutted weight, the recent Råfisklaget series, reporting kilo of liver per kilo gutted weight, and the research survey data, reporting kilo per kilo whole weight. Lower panel shows supplementary data sources on gutted weight and total length.

et al., 2012). Some large immature specimens might, however, show extended winter migrations to the coast, i.e. so-called "dummy runs", and thereby appear close to the spawning ground (Trout, 1957; Woodhead and Woodhead, 1965). The main part of the data were from the long-running report series established by the Norwegian authorities in 1859, initially named "Om Lofotfiskeriet", but renamed "Lofotfiskeriet" in 1879, "Lofotfisket" in 1922, and then "Melding fra utvalgsformannen for Lofotfisket" in 2000. However, this report series discontinued their account of landed quantities of the liver in 1990 and data for the latter period (1991–2012) was therefore obtained through Norges Råfisklag (http://www.rafisklaget.no/), commonly called "Råfisklaget" (Figure 2). Råfisklaget is the largest fishers' sales organization in Norway, administrating, among other tasks, all catches and catch statistics of cod from local landing ports under strict governmental laws and regulations.

Research survey data

A fisheries-independent liver series of NEA cod, established as part of the Institute of Marine Research (IMR) statutory acoustic spawning migration survey in the Lofoten area in March–April 1997–2013, was included to be contrasted with the corresponding commercial series in overlapping years (Figure 2). Whole body weight and liver weight were measured onboard to the nearest gramme using a motion compensated balance.

Bulk measures from the Lofoten fishery

Data presented in the yearly Official Fisheries Statistics (Anon, 1859–2012), hereafter referred to as the Fisheries Statistics, including those of Hjort (1914), were collated from bulk measures of landed cod and liver during the Lofoten fishery. To establish a coherent extension of Hjort's original time-series, the same source was consulted for 1859–1990, whereas after 1990, analogous data had to be obtained from landings data recorded by Råfisklaget (Figure 2). For the earlier period, the Lofoten area was defined by the principal communities used in the Fisheries Statistics. These included Flakstad, Moskenes, Vestvågøy, Værøy, Vågan, Røst, and Lødingen. Only NEA cod caught in the period of the Lofoten fishery, i.e. January to April, were considered.

For total landings of NEA cod, the Fisheries Statistics denote numbers of landed individuals (thousands) from 1859 to 1937 (Figure 2). In an overlapping period from 1929 to 1937, total landings were recorded both in numbers and in tonnes gutted weight, whereas after 1937, total landings were only available in tonnes gutted weight (Figure 2). Here, gutted weight excludes the head, guts, roe, and liver. Liver quantities before 1881 were logged as the number of barrels (á 116 l), whereas from 1881 to 1990, total quantities were expressed in hectolitres (100 l). The statistics from Råfisklaget used for the remaining period (1991–2012) were given in tonnes, both for the amount of cod liver and gutted weight.

Standardization of commercial Lofoten data

Hjort's (1914) original time-series on the amount of landed liver of NEA cod (1880–1912) used hectolitres/1000 fish (Figures 1 and 2). This was a convenient measure at the time because catch statistics of liver landings were recorded in volumetric units and fish in numbers. However, when extending the time-series forward in time, we found that the Fisheries Statistics switched to cod landings in gutted weight, not numbers, and this practice continued with Råfisklaget. We believe that it is more biologically meaningful to divide liver size by total body weight, i.e. to adopt the common HSI (see formal definition below).

From fish numbers to weight

For the period when gutted weight was available together with the amount of liver collected (1929–2012; Figure 2), gutted weights were multiplied by 1.5, which is the common conversion factor used to calculate total ("round" or whole) weight from gutted weight in the Norwegian cod fisheries (http://www.fiskeridir.no/fiske-og-fangst/omregningsfaktorer). For the earlier period (1859–1928), only numbers of landed cod were available in combination with the liver data. However, for the larger part of this period, matching information on fish size was found in Rollefsen (1953), who presents official catch statistics of mean gutted weight of commercially landed NEA cod in Lofoten from 1883 to 1953. Hence, numbers of cod could be converted to total weight in the period 1883–1928 using the corresponding data in Rollefsen (1953; Figure 2). However, for the years 1859–1882, data on cod size were unavailable and a proxy of bulk HSI was estimated from a linear regression (see Section "Turning hectolitres of liver into HSI") based on the period where data for both the number of fish and mean gutted weight were available (1883–1937).

From liver volume to weight

While data on liver landings from Råfisklaget (1991–2012) were presented in weight, the Fisheries Statistics (1859–1990) used volumetric measurements (Figure 2). To calculate HSI, liver volume had to be converted to liver weight. The specific density of a liver will vary due to variations in its content of fat, water, and protein, with the latter constituent exhibiting less variation (Lambert and Dutil, 1997; Skjæraasen *et al*., 2010). A liver containing no fat is expected to have a specific density of ≈1 g ml^{-1}, i.e. only water and minor amounts of protein, whereas a liver containing only fat would have a specific density of ≈0.9 g ml^{-1}, i.e. only fat and minor amounts of protein. In reality, neither extreme is likely (e.g. a fat liver will also contain some water) and the range of possible density values is therefore limited. We used a specific density of 0.96 g ml^{-1} for all years in question based on the available liver proximate composition data on captive spawning individuals of cod in moderate to good condition (Kjesbu *et al*., 1991). Hence, liver weight was estimated as 0.96 × liver volume.

Turning hectolitres of liver into HSI

For the period 1883–2012, the standard formula used to estimate the bulk hepatosomatic index (HSI_{Bulk}) was:

$$\text{HSI}_{\text{Bulk}} = 100 \times \frac{\text{total amount of liver}}{\text{total amount of fish}}, \qquad (1)$$

where both the denominator and the numerator are the measures of mass presented in kg. For the earliest part of the Fisheries Statistics time-series (1859–1882), where systematic information on NEA cod body size was lacking, we applied a somewhat different procedure to get HSI_{Bulk}. Because there exists an overlapping period in the Fisheries Statistics (1883–1937) where liver quantities are available in both l/1000 fish (denoted as $\text{Hectolitres}_{1000\ \text{fish}}$) and l/kg gutted fish (Figure 2), we utilized the linear relationship between these two measures (Figure 3) to estimate HSI_{Bulk} for the earliest period without fish weight (1859–1882):

$$\text{HSI}_{\text{Bulk}} = 2.40 + 1.236 \times \text{Hectolitres}_{1000\ \text{fish}}, \qquad (2)$$

where $r^2_{\text{adjusted}} = 0.89$ (d.f. = 54 and $p < 0.0001$). Within this particular period, observed values of $\text{Hectolitres}_{1000\ \text{fish}}$ ranged from 2.00 to 4.22 (Figure 3). For the sake of readability, HSI_{Bulk} will from here on be referred to as only as HSI, or bulk HSI if necessary to avoid confusion with individual HSI.

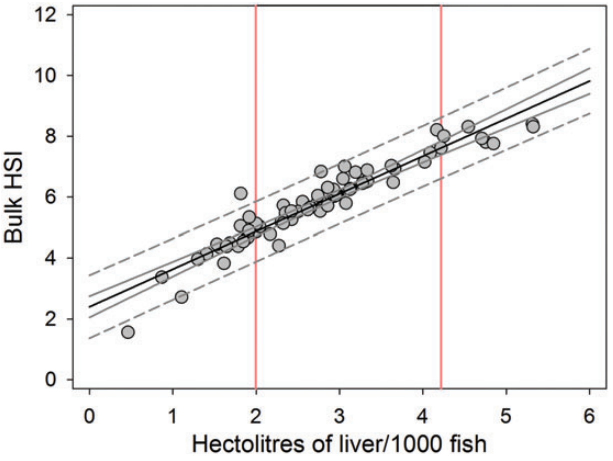

Figure 3. Linear regression between the measured amount of hectolitres of liver per thousand fish vs. the correspondingly estimated bulk HSI from the Lofoten northeast Arctic cod fishery, 1883–1937. Black solid line, regression line; grey solid lines, 95% confidence band; grey broken lines, 95% prediction band. Vertical lines show the range of values used in the prediction for the period 1859–1882.

Exploratory analyses

Fat content vs. HSI

As the fat content data in Hjort (1914) were limited, similar data from the Barents Sea and Lofoten area in 2007/2008 were consulted in Skjæraasen *et al.* (2010) to statistically relate HSI to liver "condition". In Hjort (1914), no clear statements on which methods were used to extract the fat were given, only that the content of "medicinal oil" was reliably estimated by a person named Mr P. M. Heyerdahl, personally observing "the course of the fishery". Skjæraasen *et al.* (2010) used a standard laboratory techniques of today, including extraction by ethyl acetate and spectrophotometric determination of triplicates. In our analysis, four outliers (out of 91 observations) were deleted; see applied statistical tests in Skjæraasen *et al.* (2010). Note that in Skjæraasen *et al.* (2010), data were presented as somatic HSI values, i.e. HSI = 100 × liver weight × (total fish weight - gonad weight)$^{-1}$, whereas in the present study the same data are presented as percentages of total weight, i.e. HSI = 100 × liver weight × total fish weight^{-1} [Equation (1)], to allow for direct comparisons with data from Hjort (1914). To investigate whether a change-point existed in liver fat percentage for a given HSI value, piecewise linear regression was used, where the inflection point was presumed unknown (estimated). The regression and 95% bootstrap confidence intervals (CIs) were fit using the SiZer package (Sonderegger, 2012) in R (R Development Core Team, 2013). Piecewise linear regression estimates one, abrupt change in the slope, but the data suggested that the change might be better fit by a curve. Therefore, a bent-cable regression for independent data was also fit, using the bentcableAR package (Chiu, 2012).

Trends in HSI

Basic statistics on HSI from the Lofoten fishery were reported in three different ways: (i) the HSI for each year based on the total amount of landings of cod and liver in that year (see above), (ii) the smoothed 9-year average of bulk measures (the level of smoothing was based on trials to properly account for interannual variability), and (iii) the grand mean of HSI measures for a specific time segment (change-point analysis). Change-point analysis was used to identify the location of multiple change-points, or abrupt changes in the mean level, within the HSI series. For the changepoint analysis, a Segment Neighbourhood algorithm (Auger and Lawrence, 1989) was chosen because it does not sacrifice accuracy (Killick and Eckley, 2013). Thereafter, the Akaike Information Criterion (AIC) was consulted (changepoint package in R; Killick and Eckley, 2013) to assess a penalty for the number of segments used to describe the data and thus prevent overfitting. Trends in bulk HSI were tested with the earlier mentioned piecewise linear regression package using the complete dataseries from 1864 onwards; no data existed for 1863. The annual mean HSI from the fisheries-independent survey data were compared with the commercial bulk HSI.

Predictors of HSI

Our inclusion of biometric predictors was limited to total length (TL), which is believed to have the main effect on the HSI (Yaragina, 1996, 2010; Sandeman *et al.*, 2008). Reports on TL were taken from the IMR commercial catch sampling programme, conducted between January and May in the Lofoten area from 1932 (Figure 2). To reflect the protocol of the corresponding bulk liver sampling programme, we combined TL information from all types of gears, but only used specimens classified by otolith expert readers as "certain skrei", i.e. NEA cod from the main Barents Sea area (Rollefsen, 1933, 1934). TL information was lacking for 7 years in the 1970s. The 1989 estimated length (67 cm) was omitted from the analysis as it appeared to be an outlier. Change-point analysis was performed to identify the location of changes in mean TL. The maximum number of change-points used was four based on the inspection of segment length.

Other factors that might explain the dynamics in the HSI were also investigated. The influence of ocean temperature (Sandeman *et al.*, 2008), represented by the Kola transect temperature series (hereafter Kola temperature) from the Barents Sea (0–200 m depth, 70°30′–72°30′N 33°30′E) (Boitsov *et al.*, 2012), was chosen because of its influence on prey abundance and individual growth and condition. Temperature, categorized as high (warm) or low (cold) within a year, was defined in relation to the average Kola temperature for 1900–2012, i.e. Δ_{temp} = annual temperature - mean Kola temperature. Also consulted was Godø's (2003) definition of warm and cold periods, largely based on Kola temperature, especially before 1900 when only anecdotal information on temperature was available. The North Atlantic Oscillation (NAO) winter index, established from 1899 (Hurrell *et al.*, 2003), was also included. When the NAO is in a positive phase, oceanic responses in the Barents Sea are reinforced; this typically results in increased Atlantic Water inflow, which increases both the temperature and the influx of zooplankton prey into the Barents Sea. The principal component-derived index was used instead of the station-based index because it is considered a more optimal representation of the full NAO (Hurrell *et al.*, 2013). Total spawning-stock biomass (TSB, i.e. mass of specimens aged 3 years and older) and spawning-stock biomass (SSB, i.e. mass of maturing, spawning, or spent specimens) were selected to investigate the effect of density-dependence on HSI; series for both indices were available from 1900 (Hylen, 2002; ICES, 2012). However, because of collinearity, only a few of these factors were included in the final model; TL and TSB were significantly correlated ($r = 0.39$, $p = 0.0005$), as were TSB and SSB ($r = 0.53$, $p < 0.0001$), and Kola temperature and NAO ($r = 0.36$, $p < 0.0001$). Only TL and SSB were uncorrelated ($r = 0.05$, $p = 0.689$).

Due to the collinearity of possible explanatory factors (noted above), only those that were not correlated but believed to have a relationship with the HSI were included in the same model. The effects of TSB and Kola temperature (including a lagged effect, investigated *a posteriori*) on the HSI were investigated using a GAM (Generalized Additive Model) with a Gaussian error structure and identity link. Kola temperature was included in the final multivariate model, not the NAO index because regional or local environmental effects were expected to have a greater direct effect on cod than large-scale atmospheric factors. The effect of the NAO on the HSI was investigated separately, using again a GAM with Gaussian error structure and identity link. Both the HSI and NAO data were standardized to a mean of zero and a standard deviation of one before the analysis to put the indices on a common scale. A plot of the HSI and NAO indicated a slight non-linear effect. Because this could be the result of a lagged effect in the predictor variable, the effect of a 1-year lag was also investigated *a posteriori*. GAMs were run in R (R Development Core Team, 2013) using the mgcv package (Wood, 2011). All remaining data explorations were done either with Microsoft Office Excel 2007, Systat® 13 or SigmaPlot® 12.

Results

Fat content vs. HSI

The combination of recent and historical liver fat data indicated a markedly lower HSI-specific liver fat content in Hjort (1914) than today (Figure 4). No statistical test was performed because the raw data were different in nature, i.e. bulked and individual data, respectively. Hjort's HSI data were also very restricted in range ($1.6 \leq \text{HSI} \leq 7.0$) compared with the present-day HSI values ($1.5 \leq \text{HSI} \leq 16.0$). Although both Hjort (1914) and Skjæraasen *et al.* (2010) reported the same minimum HSI, in terms of liver fat, the minimum content observed in the two studies was very

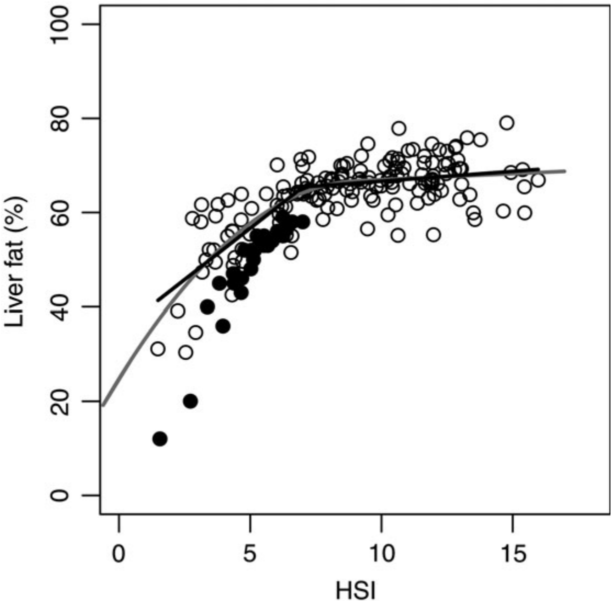

Figure 4. Relationship between historical (filled circles) and recent (open circles) HSI and liver fat content of northeast Arctic cod. Grey line is the bent-cable regression fit, while the black line is the piecewise linear regression.

different; 12 and 30%, respectively. The maximum liver content was also dissimilar; 59 and 79%, respectively.

Use of the individual data from Skjæraasen *et al.* (2010) showed an inflection point, where the growth in the percentage of liver fat reached an asymptote at ~70% (Figure 4). Both the piecewise linear regression and the bent-cable regression model indicated a change in slope (inflection point) at HSI = 7.0 (liver index = 65.4% at this point). However, the bootstrapped 95% CIs of the inflection point were wide for both models; 3.8–9.0 for the piecewise linear regression and 4.2–9.6 for the bent-cable regression model.

Trends in the HSI

The collation of information from the Lofoten fishery (Figure 2) made it possible to establish a 153-year long HSI time-series for NEA cod from 1859 to 2012 except for 1863, where no record on liver landings was found (Figure 5). These reports on the bulk HSI were centred on ≈6 (grand mean: 5.89; 95% CI: 5.70—6.09), but annual fluctuations were evident; the CV (coefficient of variation; s.d./mean) was estimated at 0.20. The most recent HSI values were comparable with the low values seen at the end of the 19th/beginning of the 20th century (Figure 5). Fisheries-independent data from the period 1997–2012 (Figure 2) were similar to the commercially based HSI and showed no evidence of contrasting values ($p = 0.063$, Wilcoxon signed-rank test), except in 2011 and 2012, when the research survey series had markedly higher values (≈1.5 per cent points; Figure 5). Excluding these 2 last years from the test, the p-value changed to 0.198. Furthermore, the mean HSI from the 2013 research survey was as high as 5.64 (Figure 5). This marked contrast with the commercial HSI series might indicate that there are differences in how livers are currently processed.

Minimum and maximum HSI values spanned a broad range of ocean temperatures. Using mean Kola temperature as reference point (1900–2012: 3.99°C), the lowest value, found within "Hjort's time-series", i.e. 1.6 in 1903, occurred when ocean temperatures were below average ($\Delta_{\text{temp}} = -0.91$°C). The second lowest HSI value of 2.7 in 1883 occurred before the Kola series began, but was most likely during a period of ocean cooling (Godø, 2003). The next three lowest HSI values appeared both during warm and cold ocean periods: 2012 (HSI = 3.3, $\Delta_{\text{temp}} = 1.37$°C), 1904 (HSI = 3.4, $\Delta_{\text{temp}} = -0.43$°C), and 2011 (HSI = 3.5, $\Delta_{\text{temp}} = 0.38$°C). The maximum HSI appeared in 1953 with a record of 9.1, but this was during a cool ocean phase ($\Delta_{\text{temp}} = -0.20$°C).

Although the HSI oscillated considerably over the time-series, some broader patterns were discernible after smoothing (Figure 6), the HSI declined from the start of the time-series in 1859 until the 1880s, when it remained low. Then, the HSI increased noticeably from the 1920s up to the 1950s, after which it remained relatively high until the mid-1970s before decreasing. The change-point analysis on the complete HSI series identified five different periods (Figure 6), the respective grand means being: (i) 1859–1880: 6.1; (ii) 1881–1919: 5.0; (iii) 1920–1974: 6.8; (iv) 1975–2003: 5.5; (v) 2004–2012: 4.4. Exclusion of predicted values (1859–1882) from the analysis did not affect the location of the four later segments.

Kola temperature and the HSI, both smoothed over 9 years, varied in close synchrony until the 1970s, but then the Kola temperature increased with no comparable response in the HSI (Figure 6). From the mid-1980s, the two series have trended in opposite directions. The piecewise linear regression analysis (1864–) showed a change in the annual trend in the HSI in 1954 (97.5% CI: 1951–1966), which occurred shortly after a decline in the Kola temperature (1950–pre-1990).

Predictors of the HSI

The body size of NEA cod fluctuated markedly (Figure 7a), and this dynamic had a significant effect on the HSI (Figure 7b;

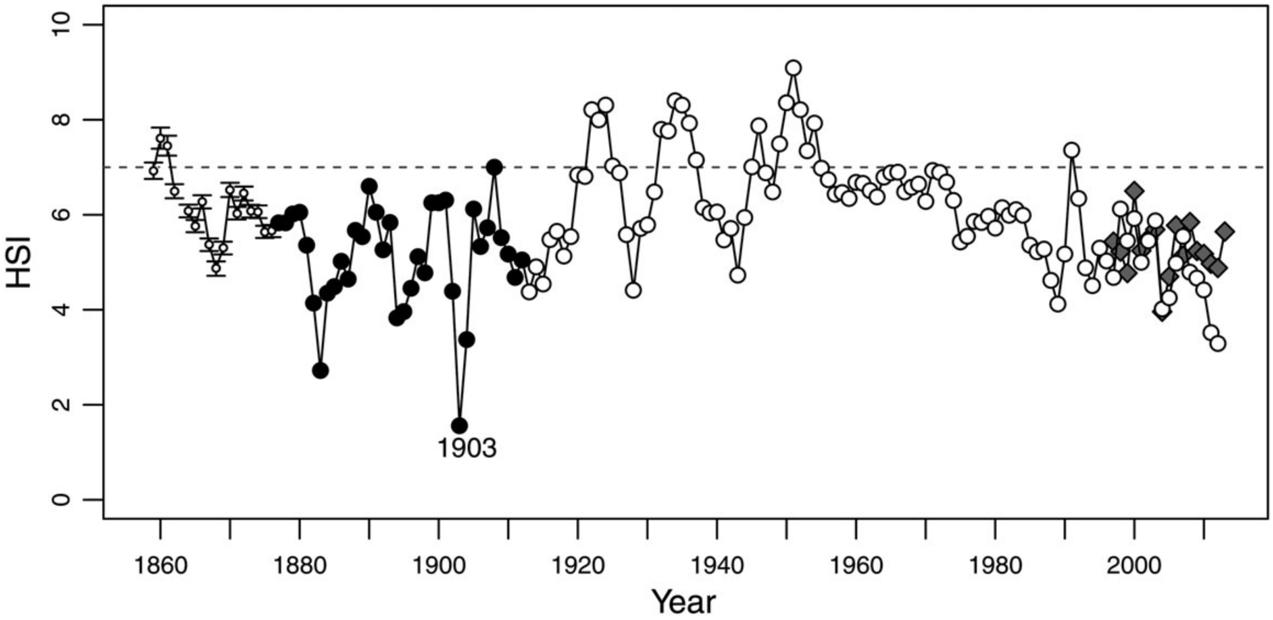

Figure 5. Annual variation in the northeast Arctic cod bulk HSI from the Lofoten fishery (1859 – 2012; circles) and the mean HSI (diamonds) from the Institute of Marine Research (IMR) Lofoten research survey (1997 – 2013). Values for 1859 – 1876 were estimated and include the 95% CI of the estimates. Black circles indicate the period of Johan Hjort's investigations. The dotted line (HSI = 7.0) is the inflection point from the piecewise and bent-cable regressions (see Figure 4).

$r^2_{\text{adjusted}} = 0.25$, $p < 0.0001$, linear regression). Change-point analysis indicated four periods in TL size [grand mean (cm): (i) 1932–1946: 86.1; (ii) 1947–1965: 90.2; (iii) 1966–1986: 81.8; (iv) 1987–2012: 79.0 (Figure 7a)]. Generally, the HSI increased with the mean TL, but the last 2 years (2011 and 2012) had the lowest recorded HSI, although the mean TL in these years was not atypical (grand mean entire period = 83.7 cm).

From 2010, TSB has been high but within the normal range seen within the time-series, whereas SSB has been at a historical high (above 1.2 million tonnes; Figure 8a). No evidence of a relationship between HSI and SSB was present. Both TSB and Kola temperature were positively related to the HSI, but each factor explained less than the mean TL, and their contribution was insignificant ($p > 0.05$) if combined with TL. TSB regressed on the HSI showed an r^2_{adjusted} of 0.13 ($p < 0.0001$, linear regression; Figure 8b), whereas the % deviance explained for HSI vs. Kola temperature was 10.3 [GCV (Generalized Cross-Validation) score = 1.44, $p = 0.03$, GAM; Figure 8c]. Kola temperature appeared to be positively related to the HSI at temperatures below 4°C, but negatively above 4°C, i.e. there were weak indications of a convex response curve (Figure 8c). Time-lags were investigated, but lagged temperature was not found to be significantly related to changes in the HSI. In the multivariate model, the HSI was positively related to both TSB ($p < 0.0001$) and Kola temperature ($p = 0.009$) but a large amount of variability was left unexplained by the GAM (% deviance explained = 24.2, GCV score = 1.29), indicating that other factors may be important. The winter NAO index did not predict changes in the HSI ($p = 0.10$) but there was a marginally significant linear relationship ($p = 0.045$) at a lag of 1 year (Figure 8d).

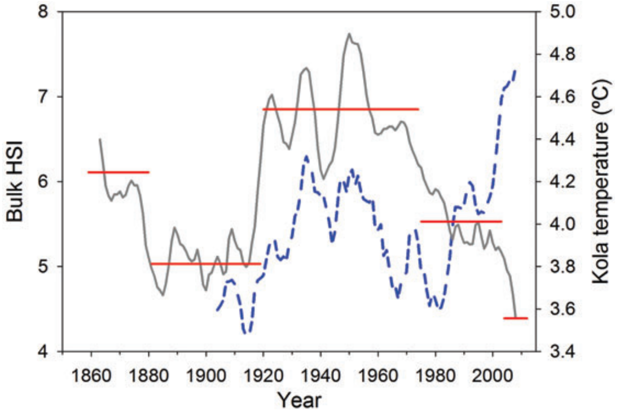

Figure 6. Temporal trends in 9-year smoothed HSI (solid line) and Kola temperature (broken line). Horizontal lines are the grand mean HSI for a specific period (segment) located by change-point analysis.

Discussion

One might wonder if Johan Hjort, when collating and interpreting his liver time-series (1880–1912) on NEA cod from the Lofoten area, was aware that Ketil Motzfeldt's initiative of Fisheries Statistics records (1859–1879) existed. If Hjort had elongated his time-series to cover 54, instead of 33, years, he might have been in a better position to fully judge the "condition" of NEA cod within his period of interest. Condition was generally on the poor side over the longer period, i.e. not only in 1903 as stated in his book, and included much larger interannual variability. The year 1903 is worth special attention for both biological and social reasons; the

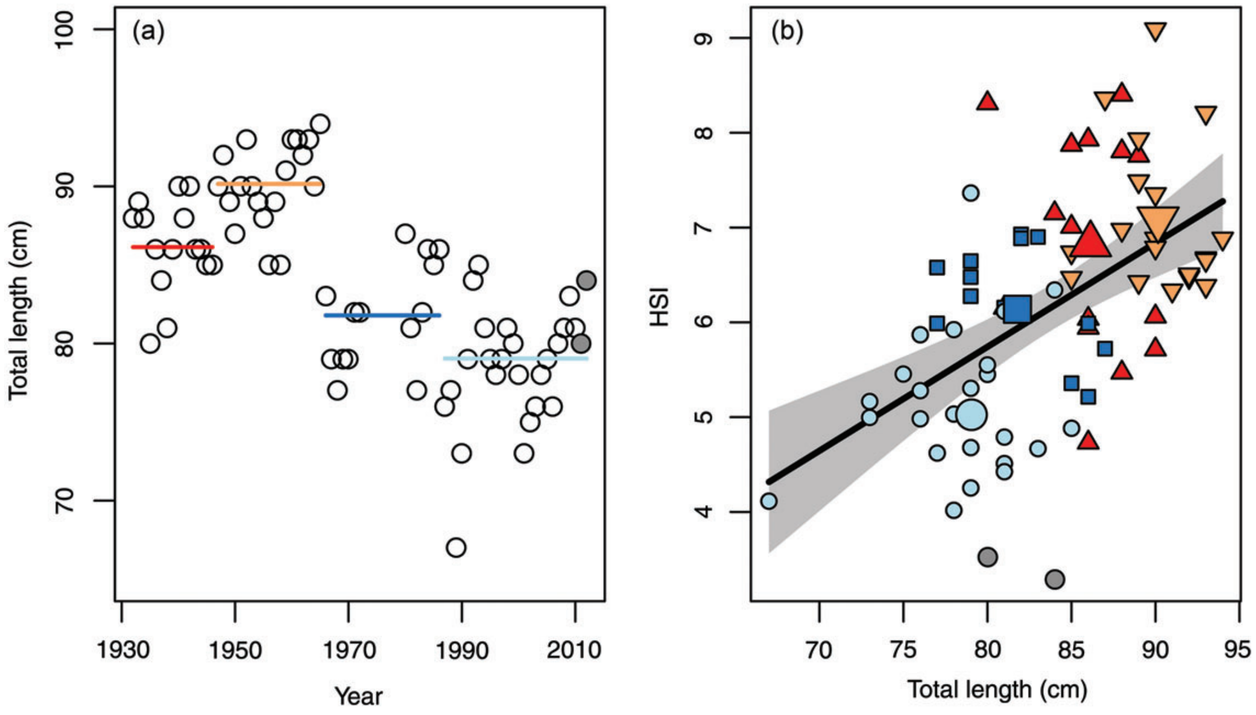

Figure 7. Variation in northeast Arctic cod (a) mean TL, 1932–2012 and (b) the resulting relationship with the HSI. Horizontal coloured lines are the average TL per period identified by change-point analysis, whereas the solid black line is the linear relationship with the 95% confidence band (shaded area). Grey circles in both panels are the years 2011 and 2012. Symbol colour in (b) corresponds to segment line colour in (a). Large symbols in (b) are the mean HSI for each period as defined in (a).

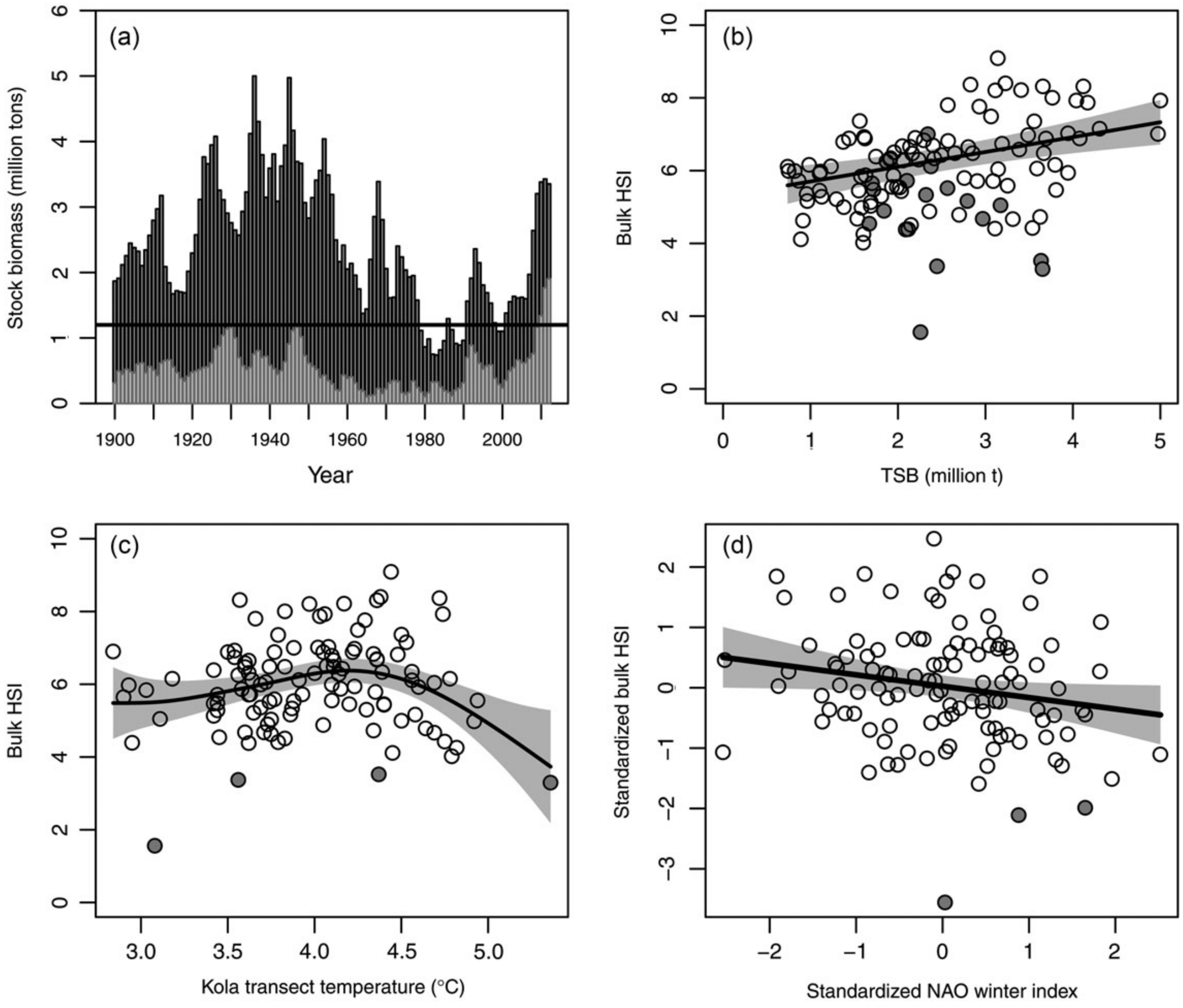

Figure 8. Trends in (a) total-stock (black columns) and spawning-stock biomass (grey columns) of northeast Arctic cod, (b) HSI vs. total-stock biomass (TSB), (c) HSI and Kola temperature, and (d) standardized HSI vs. standardized NAO winter index (lagged by 1 year). Line in (a) refers to the maximum spawning-stock biomass through 2009, i.e. 1.2 million tonnes. Lines in (b)–(d) are the fitted regression or GAM models, whereas the shaded areas are the 95% confidence band. Grey circles in (b)–(d) indicate the low HSI from years 1903, 1904, 2011, and 2012.

"revolt in Finnmark" (Northern Norway) took place that year, when angry fisher attacked the local whale oil factory and blamed this industry for the poor cod fishery (Hanssen, 1963). The more likely reasons for the failure in the cod fishery were a collapse in the capelin stock and invasion of seals to the coast (Hanssen, 1963). In other words, a situation resembling "the ecological crisis in the Barents Sea" seen in the late 1980s (Hamre, 1994). The extremely low HSI of 1.6 in 1903 could be argued to be unrealistically low (Figure 5), but such values are also detected in more recent articles, for both individuals (Skjæraasen *et al.*, 2010) and length classes of smaller cod (TL $\leq$ 80 cm; Sandeman *et al.*, 2008; Skjæraasen *et al.*, 2012). Likewise, the fat content of 12% in 1903 is probably not a reporting mistake (Kjesbu *et al.*, 1991), especially after accounting for the inefficient fat extraction procedure at Hjort's time, where it was several per cent points less effective than in today's laboratory (Figure 4). Extreme low HSI values appear when spawners are both small in size and in poor condition (Hjort, 1914), and high HSI values result when the opposite is the case (Marshall *et al.*, 1998). Note also that the 1903 HSI value was linked to an extremely cold year, which may have influenced individual size and condition in that year. A useful cut-off between relatively poor and good condition for NEA cod might be the threshold HSI = 7, i.e. the inflection point in the liver fat content curve (Figure 4). However, this point value should not be taken too literally as the statistical analyses showed that variance in liver fat content at this threshold was moderately large. Furthermore, the average HSI is typically around 6; higher average values are rare and were found mainly in the 1920–1950s in some of the years (Figure 5). Taken together, one's perspective regarding trends and magnitude of change is very much dependent upon the length of the time-series, but extreme values are important to address and clarify main causal factors.

The liver data in the 1914 publication of Johan Hjort inspired us to establish the current series; his data formed a natural "bridge" between the earliest and the latest Fisheries Statistics data. The presented biological series, 1859–2012; 153 years (no data in 1863), is probably one of the longest in the world, although there are examples of others, e.g. White Sea herring (*Clupea pallasi marisalbi*) catch statistics that go back to the 1780s (Lajus *et al.*, 2007). This statement ignores species of no commercial interest, as well as proximate (e.g. Øiestad 1994), anecdotal information (Kurlansky, 1997) and limited or non-sequential data. To create this long series, we had to assume that the manner and frequency of how liver was extracted from and landed together with cod were similar throughout the time-series. This latter view was challenged by the introduction of the fisheries-independent HSI series; relatively less liver is probably landed when the fishing ground is densely packed with spawners, as seen in recent years (see below). This issue should be looked into more closely in future studies.

Although we focused on a characteristic life-history metric, i.e. it's liver size, of a capital spawner (Alonso-Fernandez and Saborido-Rey, 2012), the Fisheries Statistics have also been used to document the loss of spawning fields in southern Norway, i.e. a northerly shift, over time (1866–1969; Jørgensen *et al.*, 2008; Opdal, 2010). The Fisheries Statistics also form a central input in the unique series of NEA cod population dynamics (1900-present; Hylen, 2002), which shows large fluctuations in stock size and recruitment. Furthermore, series from stock assessments (ICES, 2012) clarify that both the SSB and TSB of today are among the highest in history, particularly for SSB, which is the highest recorded. This high biomass (Figure 8a) appeared in exceptionally warm waters (Figure 6), although the causal mechanisms are obviously complex. The temperature series used in our analyses was chosen because of its high quality (length and completeness) and relevance (reflecting both temperature *per se* and advection of Atlantic water masses; Boitsov *et al.*, 2012). The same argument applies to the NAO index, although reflecting instead westerly wind in the North Atlantic, which is known to influence multiple factors that might affect fish population dynamics (Hurrell *et al.*, 2003).

The lack of any potentially suitable explanatory time-series before 1900 makes any advanced exploratory analysis for the whole length of the present NEA cod liver index series highly challenging or speculative. However, for the sake of clarity metrological data as such can be traced several hundreds of years back in time (Parker *et al.*, 1992), but is difficult to compile such series for the area near Northern Norway. We therefore restricted the analysis to a limited number of series, all commencing around 1900, i.e. Kola temperature, SSB, TSB, and the NAO index, which starts before our series and continuing up today. A long list of other less data-rich covariates, not considered here, may also be expected to influence the HSI, such as sex ratio (Marshall *et al.*, 1998; Yaragina, 2010), length and age at maturity (Jørgensen, 1990; Nash *et al.*, 2010), capelin abundance (Marshall *et al.*, 1998; Sandeman *et al.*, 2008), migration distance (Jørgensen *et al.*, 2008; Opdal, 2010), and, possibly, fisheries-induced evolution (Heino *et al.*, 2002; Olsen *et al.*, 2004; Jørgensen *et al.*, 2007, 2009).

The HSI vs. Kola temperature analysis (Figure 8c) resembles a "dose–response curve", as seen in physiology; however, only a small amount of the deviance was explained, which indicates that other factors might be responsible for the observed changes. Because individual HSI can change rapidly with food consumption and is heavily influenced by fish size, care must be taken not to over-interpret these results. Nevertheless, Kola temperature has been shown to not always have a positive effect on the HSI (Sandeman *et al.*, 2008), whereas we have shown that large-scale atmospheric factors (that influence many other factors) do not appear to play a strong role in determining HSI. Godø (2003) grouped temperature into likely warm and cold periods, beginning in 1866 (see also Opdal, 2010). The last cold period ended in the mid- to late 1980s and the Barents Sea is currently in a warm period. The higher HSI was typically associated with warm periods, and cold periods with a lower HSI, but the recent HSI values are surprisingly low, contradicting this pattern.

TSB, but not SSB, appeared to have a weak relationship with the HSI. This result may be an artefact of the strong correlation between TSB and TL, which has a strong relationship with the HSI. TL clearly began to decline after 1965 (Figure 7a), but the HSI began its downwards trend in 1954, although still being reasonably high up to the mid-1970s (Figure 6). Several things were happening in this period that might be responsible for the trends. The temperature in the Barents Sea was declining and cold periods appear to indicate the lower HSI. But perhaps more importantly, the effects of industrialized fishing began to change the demographic structure of the cod population (Jørgensen, 1990). With declining fish size, the HSI continued to decline. Hence, the remarkably close association seen between HSI and Kola temperature, provided smoothing both dataseries (currently over 9 years), from 1900 and up to this time vanished. Because the relationship between size and HSI is much stronger than that with temperature, the HSI continued to decline with size even after temperature shifted to a warm phase. The effects of temperature on the HSI are weak and the conclusions drawn regarding its effects are, at best, speculative, therefore we argue that the link between size and HSI appears currently to be the key to HSI dynamics. What causation that is behind this association is an interesting topic for future work.

In summary, we have successfully established an extremely long time-series but firm conclusions regarding potential environmental stressors, demographic factors, or evolutionary effects influencing HSI must be postponed until more in-depth analyses. The use of commercial catch statistics obviously has great merits because of their uninterrupted annual resolution and massive collection programme within a rather restricted season and geographical area.

Acknowledgements

We are most grateful to the secretariat at Norges Råfisklag (Råfisklaget), in particular Gunnar Johnsen, for providing us with NEA cod catch metrics over the last decades, and to Knipovich Polar Research Institute of Marine Research and Oceanography (PINRO), Murmansk, Russia, for giving us access to the Kola temperature time-series. Thanks also go to the librarians Wencke Vadseth (retired) and Brit Skotheim at the Directorate of Fisheries' Library, Bergen, for helping us locating Fisheries Statistics reports and other historical literature. The following projects writing supported this work: "The effect of climate change on spawning performance and survival of early life stages in North Atlantic teleosts" (IMR project no. 13710), Adaptive Management of Living Marine Resources by Integrating Different Data Sources and Key Ecological Processes (IMR and CEES) [The Research Council of Norway (NFR), 200497], and The Value of an Egg: Towards Operational Models of Fish Eggs and Larvae along the Norwegian Coast (Uni Research Computing) (NFR, 204031).

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Handling editor: David Secor

ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2064–2087. doi:10.1093/icesjms/fsu037

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

A review of early life history dynamics of Barents Sea cod (*Gadus morhua*)

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Ottersen, G., Bogstad, B., Yaragina, N. A., Stige, L. C., Vikebø, F. B., and Dalpadado, P. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). – ICES Journal of Marine Science, 71: 2064–2087.

Received 20 August 2013; accepted 13 February 2014; advance access publication 1 April 2014.

The Barents Sea stock of Atlantic cod (*Gadus morhua*) is currently the world's largest cod stock. It is also a stock for which long time-series are available and much research has been carried out. With this review, we wish to present an overview and evaluation of the knowledge on Barents Sea cod early life dynamics. The focus is on the effects of the biotic and abiotic drivers, which jointly determine the strength of a year class. A stage-by-stage approach is employed. We summarize and assess the significance of the different processes described in the literature to be at play during each specific life stage, from spawning stock, through eggs, larvae, and pelagic juvenile, to demersal juvenile and recruitment at age 3. Also Russian work is included, some of which until now has not been available to non-Russian readers. Physical drivers examined include sea temperature, advection and dispersal, wind-induced turbulence, and light. Biotic mechanisms studied range from maternal effects and skipped spawning in the adult stock through egg quantity and quality, to prey availability for the larvae and effects of cannibalism on the juveniles. Finally, we evaluate the main hypotheses put forth by Johan Hjort a hundred years ago in the light of our synthesis of present knowledge. A main conclusion is that it is unlikely that there is any one single life stage during which recruitment with any generality is determined.

Keywords: Barents Sea, cod, early life history, *Gadus morhua*, Johan Hjort, recruitment, year-class strength.

Introduction

This review

Contrary to most other commercially exploited fish stocks, the abundance of the Barents Sea cod (*Gadus morhua*) stock has been close to the historical maximum during recent years and simultaneously its habitat during summer feeding season has expanded eastwards and northwards well beyond what has ever been recorded earlier. The stock is also among the most thoroughly studied worldwide. Not least has a lot of attention been directed towards the biotic and abiotic drivers influencing early life history dynamics. In combination, they determine the strength of a year class, including recruitment, i.e. the abundance of the offspring from a given year surviving to enter the fishery. Still, no comprehensive review of the sizeable literature on this topic has yet been performed for Barents Sea (BS; also known as Northeast Arctic or Arcto-Norwegian cod). [We deliberately avoid both of these more established names. We find "Northeast Arctic cod" geographically misleading since the stock in question does not inhabit the Arctic Ocean, nor Arctic water masses. There is also a danger of confusion with "Arctic cod", which may refer to either of the species *Arctogadus glacialis* or *Boreogadus saida*. Although "Arcto-Norwegian cod" dates back at least to Sund (1927a, b), we find it somewhat strange and nationalistic. Most other cod stocks are unambiguously named from the sea or area they inhabit (North Sea cod, Georges Bank cod, Southern Gulf of St Lawrence cod, etc.)].

Here we undertake such a literature review. Also Russian work is included, parts of which until now has not been available to non-Russian readers. Throughout the bulk of the paper, we employ a stage-by-stage approach, summarizing and assessing the significance of the different processes described in the literature to be at play during each specific life stage. We also discuss the part of the literature on BS cod that by statistical analysis examines links between the environment and abundance at the recruitment stage. Finally, we evaluate the main hypotheses of the godfather of fish population recruitment science, Johan Hjort, in the light of our synthesis of present knowledge of recruitment to the BS cod stock.

Background to fish population recruitment in general

Since Hjort's seminal work was published 100 years ago (Hjort, 1914), the pursuit towards understanding what regulates variability in recruitment of commercially exploited fish populations has been a key issue in quantitative fisheries science. The number of individuals in an exploited fish stock is determined by the balance of losses from natural mortality, predation, and fishing, and the gains from the addition of new individuals to the population. Within a single stock, a management unit where the exchange of individuals with other stocks generally is assumed to be negligible, the only source of new individuals is through the reproductive process, i.e. recruitment. Therefore, recruitment places a firm constraint on the number of individuals that can potentially grow to maturity (Payne *et al.*, 2009). These facts "naturally lead us to enquire into the causes, or better, the natural phenomena which occasion these peculiar fluctuations in the renewal of the stock; the hydrographical or biological conditions which give rise to the occurrence of rich or poor year classes of fish" (Hjort, 1914). However, warns Hjort (1914), "the problem is one of unquestionable difficulty, embracing as it does all the conditions which in any way affect the fish from the egg stage to the time when they are caught".

The role of recruitment towards regulating fish population abundance fluctuations varies considerably between species and stocks (according to, for example, spawning strategy, longevity, and variable vs. more stable environments). Still, the general importance is high as shown, for instance, in a simulation study by Shelton and Mangel (2011). Here, the main drivers of temporal fluctuations of harvested fish populations in a variable environment were examined across a global sample of fish species. Their results show that the coefficient of variation of the biomass of a fish population is relatively insensitive to the variability in natural and fishing mortality in adults, while variability in recruitment contributes substantially more (Shelton and Mangel, 2011).

Intuitively, there should be a quantitative relationship between the mature population and the recruits, i.e. stock–recruitment curves. However, although strong recruitment does tend to co-occur with high spawner abundance (Myers and Barrowman, 1996), the stock–recruitment relationship in marine fish is frequently weak (Hilborn and Walters, 1992; Koslow, 1992) and, despite progress, especially the forecasting of recruitment remains a formidable challenge (Houde, 2008). Furthermore, it now seems evident that the facts regarding the stage at which year-class-strength is determined are less clear than proposed by Hjort (1914) in his first hypothesis. This, the Critical Period Hypothesis, states that variation in year-class strength mainly results from changes in the availability of planktonic food for fish larvae after exhaustion of their yolk supply. Hjort places this firmly within what later would be termed a match–mismatch context (*sensu* Cushing, 1966, 1990): "It may well be imagined, for instance, that a certain—though possibly brief—lapse of time might occur between the period when the young larvae first require extraneous nourishment, and the period when such nourishment is first available. If so, it is highly probable that an enormous mortality would result. It would then also be easy to understand that even the richest spawning might yield but a poor amount of fish, while poorer spawning, taking place at a time more favourable in respect of the future nourishment of the young larvae, might often produce the richest classes. In this connection it must be remembered that one single cod may spawn millions of eggs" (Hjort, 1914).

Fish typically develop through several stages during early life and different mechanisms may dominate at any single stage. Often, most of the variability in pre-juvenile survival is accounted for by density-independent environmental factors (Houde, 2008). Paleo-record studies on fish abundance variability before the onset of extensive fishing indicate the importance of environmental factors for population regulation (Emeis *et al.*, 2010; Finney *et al.*, 2010). On the other hand, density-dependent survival in the (late) juvenile phase is also generally believed to be of key importance in regulating the size of fish populations (Rothschild, 1986; Vincenzi *et al.*, 2012). However, as pointed out by Sakuramoto (2005) and Nash *et al.* (2009), there is still considerable debate concerning juvenile regulation and density-dependent compensatory mechanisms that results in stock–recruitment relations of, for example, the Ricker (overcompensatory) or Beverton–Holt type (Ricker, 1954; Beverton and Holt, 1957).

Early life history of the Barents Sea cod stock: setting the scene

The BS cod inhabits the Barents Sea, an open Arcto-boreal shelf sea of around 1.5 mill km^2 situated off the Northeast Atlantic, north of Norway and northwestern Russia between around 70° and 80°N (Figure 1). The biology of the stock is thoroughly described by, for example, Yaragina *et al.* (2011). BS cod normally reach maturity at an age of 6–9 years. Mature fish undertake extensive southwards upstream spawning migrations during winter–spring to patchy spawning banks along the Norwegian coast (Opdal *et al.*, 2008). It is possible for the fish to make use of occasional countercurrents when and where such conditions are available. It is known that the currents in the region are very dynamic and the velocity field is subject to large and frequent fluctuations (Ingvaldsen *et al.*, 2004).

During April–August, eggs, larvae, and later juveniles are transported north- and eastwards in the upper water layers by the Norwegian Atlantic Current and the Norwegian Coastal Current (Table 1). By August–September, they have reached the so-called 0-group stage and are spread in the upper 100 m all over the southern Barents Sea and off Svalbard, 600–1200 km from their spawning grounds (Figure 1; Ellertsen *et al.*, 1989; Eriksen *et al.*, 2011). During autumn, the 0-group fish descend towards the deeper layers, and at age 1–3, the cod are found both at the bottom and in the midwater layers (Table 1). In the following period, they are subject to considerable predation (cannibalism) by older conspecifics (Yaragina *et al.*, 2009). BS cod start recruiting to the fishery at age 3.

Stage-by-stage review of factors affecting BS cod recruitment

Table 2 gives an overview of properties and mechanisms suggested to impose interannual variability in recruitment of BS cod through affecting survival at a given stage. A conceptual Paulik diagram (Paulik, 1973) shows the factors we suggest to be the most important in determining survival from one stage to the next for the BS cod, from spawning stock through the egg, larval, and juvenile stages to recruitment at age 3 (Figure 2).

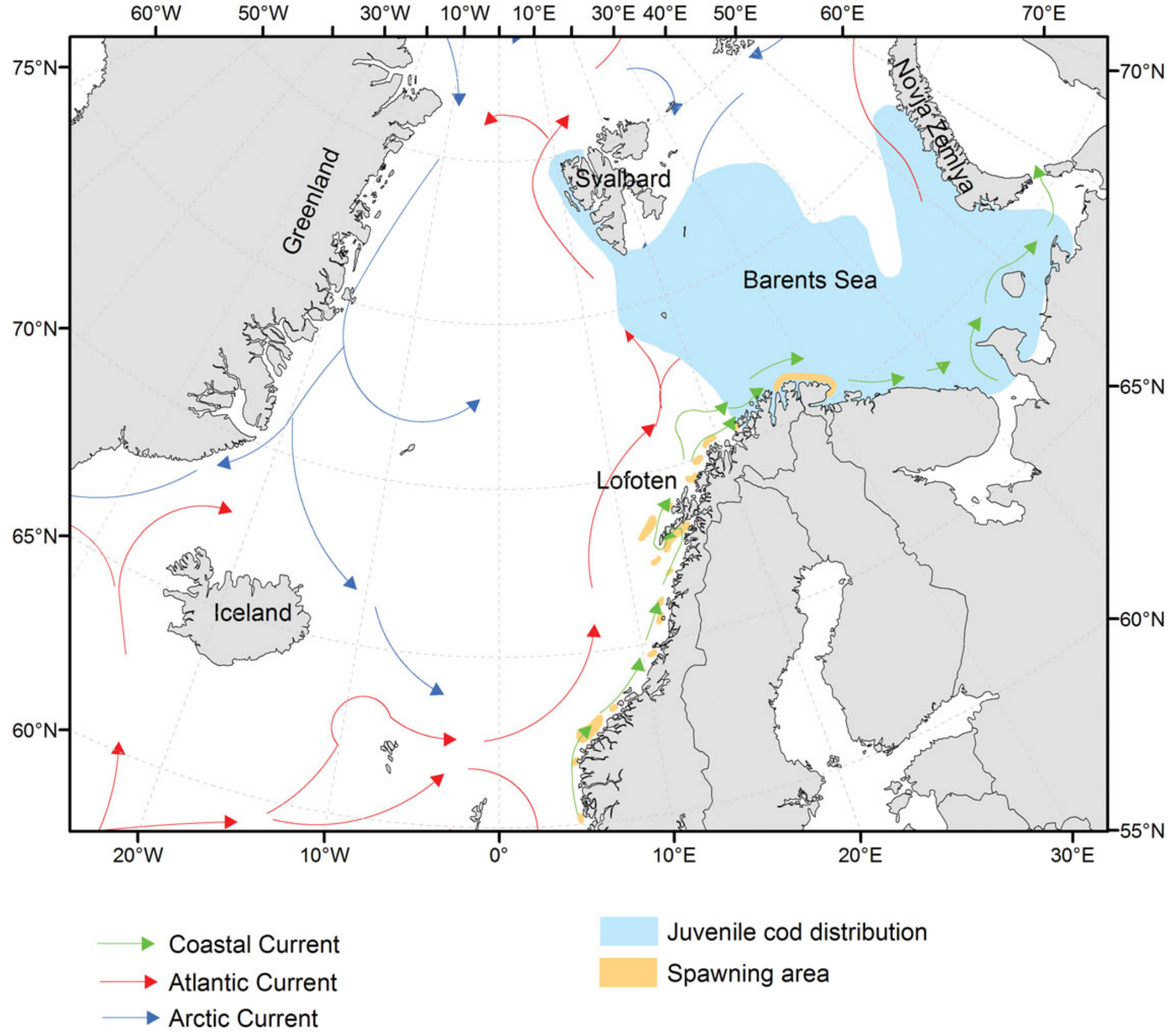

Figure 1. The Barents and Nordic Seas with spawning grounds and extent of juvenile distribution of Barents Sea cod. The arrows indicate the dominating surface currents.

Spawning stock

Spawning-stock biomass

A comparative analysis by MacKenzie *et al.* (2003) suggests that the BS cod produces a high biomass of recruits per spawning-stock biomass (the aggregated weight of mature fish in a stock, SSB) compared with other North Atlantic cod stocks, suggesting a high carrying capacity for recruit production and survival. Even so, its productivity, in terms of the surplus production per unit biomass, is low (Dutil and Brander, 2003). This is related to the slow growth and late maturation of this stock compared with other cod stocks (Brander, 1994, 1995). As already mentioned is the case for many stocks of marine fish, the relation between SSB and recruitment is weak for BS cod (Ottersen and Sundby, 1995; Marshall *et al.*, 2000; Borisov *et al.*, 2006). A large fraction of the interannual variability in year-class strength being determined by other causes. This was noted already by Hjort (1914) who observed that in 1904, there were strong year classes of all the main spring-spawning species off northern Norway (i.e. cod, haddock *Melanogrammus aeglefinus*, and herring *Clupea harengus*), suggesting strong simultaneous influence of some factor other than stock size. At that time, the fish stocks were likely close to unaffected by fisheries such that their egg production always was sufficient for stock reinforcement. On the other hand, during the second half of the 20th century when prolonged depletions and structural changes in fish stocks as a result of intensive (and often selective) fishery became more evident, a need to take the SSB effect on recruitment into consideration developed.

Within the precautionary approach to fishery management paradigm, a reference point for the bottom limit of SSB (B_{lim}) is generally set. If the spawning stock falls under B_{lim}, it is assumed that there is great chance of poor recruitment. The precautionary approach implies that the stock should be kept well above B_{lim} and so a higher precautionary level (B_{pa}) is set, which gives reasonable certainty that the stock will stay above B_{lim}. Estimating the level of SSB beyond which recruitment is impaired is one of the biggest challenges for fisheries science. More often than not setting SSB-based

Table 1. Important early life events for BS cod.

Early life event	Age	Date	Distribution	Additional information
Spawning	0	Mid February–early May	Patchy areas close to the coast of mid and northern Norway	Spawning depth 60–150 m
Hatching of eggs	2–5 weeks	Late April (average)	The progeny drift north- and eastwards with the prevailing currents Prolonged retention in eddies may occur	Development time to hatching is strongly dependent on temperature
Switch to exogenous feeding	3–6 weeks	Early May (average)		The newly hatched larvae have a yolk-sac with nutrition for 5–7 d
Metamorphosis	2–3 months	June (average)		For the stage after the transition from larva all the terms "early juvenile", "post larval", "prejuvenile", or "metalarva" have been used
Bottom-settlement	5–6 months	September–October (average)	Throughout the Atlantic water masses of the Barents Sea and west of Svalbard.	Switch from pelagic to more demersal habitat At this stage, the juveniles are termed "0-group"

Information from ICES (2005) and Yaragina *et al.* (2011). The terms "early juvenile" (e.g. Helle, 2000), "post larval" (Bjørke and Sundby, 1984), "prejuvenile" (Hardy, 1978), or "metalarva" (Snyder, 1976) have all been used for the phase of a fish's life following metamorphosis.

limit reference points is more art than science (Marshall *et al.*, 2006). The currently used biological reference points for the BS cod stock ($B_{\rm lim} = 220\,000$ t and $B_{\rm pa} = 460\,000$ t) were first applied in 2003 (ICES, 2003). The high level of fish exploitation in the 1960–1980s led to SSB frequently dropping below $B_{\rm pa}$ and even $B_{\rm lim}$. This high exploitation level did not allow the population to realize its potential for growth; it substantially exceeded the value corresponding to the maximum productivity of the stock (Kovalev and Bogstad, 2005). The SSB has been above $B_{\rm pa}$ since 2002 and is now at around 2 million t, the highest since the records started (officially in 1946, but the present SSB is also greater than seen in the reconstruction back to 1913 by Hylen, 2002).

One general reason for the weak SSB–recruitment relation may be that SSB is not a good representation of total egg production (TEP, the total number of eggs spawned by a population during the spawning season of a given year, equivalent to population fecundity). Indeed, Marshall *et al.* (1998) provided evidence for TEP being superior to SSB in predicting abundance at age 0 for BS cod, thus enabling better recruitment predictions as well as improving the ability to identify which factors affect prerecruit survival. TEP was estimated using acoustic estimates of total abundance and demographic information from trawl sampling in combination with year-specific fecundity–length relationships. Further, Marshall *et al.* (1999) showed how TEP could be accurately estimated when information on lipid content is available.

More comprehensive measures of reproductive potential than SSB (e.g. female-only spawner biomass or TEP) might explain more of the recruitment variation. For example, during 1980–2001, the BS cod TEP fell below the safe biological limit level more frequently than SSB, suggesting that using SSB as the measure of stock reproductive potential may have led to overly optimistic assessments of stock status (Marshall *et al.*, 2006). TEP may vary through changes in key reproductive parameters, not captured by the size of the SSB, like age, size, or condition (Kjesbu *et al.*, 1991). Variations in these parameters may affect reproduction through phenotypic, quantitative aspects encompassing the maturation process and the produced numbers of eggs. Several parental effects may be important for recruitment. For example, females in poor condition may skip spawning (Jørgensen *et al.*, 2006; Skjæraasen *et al.*, 2012). Further, fishing may have caused genetic changes in the BS cod stock. Also, changes in spawning location or timing may affect early survival and potentially recruitment. In the following, we will examine each of these factors.

Maternal effects

Maternal effects may be defined as non-genetic reproductive traits (i.e. tactics) driven by an individual's status—such as its size relative to other conspecifics, or internal energy level (Green, 2008). These effects may in turn have effects on offspring size, condition, and viability (Solemdal, 1997). A number of publications, reviewed by Berg and Finstad (2008), suggest that maternal fitness, defined as offspring fitness times number of offspring, changes over the lifespan of an adult. Indeed, some experimental studies suggest that larger (and implicitly older), more experienced female Atlantic cod tend to have a disproportionably higher reproductive capacity than younger and smaller recruit spawners, due to both a larger number and more viable offspring (Kjesbu *et al.*, 1992, 1996; Solemdal *et al.*, 1995; Marshall *et al.*, 1998). First-time cod spawners breed for a shorter period, produce fewer egg batches with smaller eggs that experience lower fertilization and hatching rates than do second-time spawners (Trippel, 1998). The longer spawning period of repeat spawners may be advantageous because the extended period of release of eggs into the variable environment could improve the probability of a temporal match between first-feeding larvae and abundant prey (Hjort, 1914; Trippel, 1998; Durant *et al.*, 2007).

However, a mesocosm experiment involving 3876 cod larvae and juveniles from 26 families of recruit and repeat (second-season) spawners originating from the Barents Sea gave a seemingly contrary result. The larvae from recruit spawners were significantly longer and heavier at hatch and throughout the 10 weeks, the experiment lasted (Clemmesen *et al.*, 2003). However, no difference in nutritional condition (measured by RNA:DNA ratio) was detected between the two groups of offspring. Further, it should be noted that laboratory environments are different from natural conditions

Table 2. Properties and mechanisms suggested to impose interannual variability in survival of BS cod at the given stage, ultimately affecting recruitment.

Life stage	Property/mechanism	Explanation (our view)	Key papers
Spawning stock	Biomass (SSB)	Weak SSB – recruitment relation well documented	Myers and Barrowman (1996), ICES (2003), Borisov *et al.* (2006)
	Total egg production	Better estimator of abundance at egg stage and later than SSB	Marshall *et al.* (1998, 2006)
	Maternal effects	Effects shown in laboratory. Intuitively, the condition of mother fish should affect offspring, but not proven at population level. Indirect effects difficult to trace over several consecutive stages	Solemdal *et al.* (1995), Kjesbu *et al.* (1996)
	Paternal effects	Unknown for BS cod. Likely of less importance than maternal effects. Juvenation may cause shorter spawning season	Nash *et al.* (2008)
	Skipped spawning	The phenomenon is well documented, time series of estimates of the frequency exists for 1984–2006. Closely linked to individual female energy reserve. Expected to be a significant source for variation in early life abundance	Skjæraasen *et al.* (2009, 2012), Yaragina (2010)
	Proportion of females	Strong fluctuations at population level documented. Likely a significant source for variation in early life abundance. Juvenation of the stock leads to male-biased ratios	Ajiad *et al.* (1999), Marshall *et al.* (2006)
	Age structure	Pronounced changes well documented from 1913 to present. Strong juvenation from around 1950–1990s. Age diversity increased during last 5 years. Mean age will likely increase over the next years. No clear effect on recruitment documented	Nilssen *et al.* (1994), Ottersen *et al.* (2006)
	Fisheries-induced evolution	Fishery has likely, but not conclusively caused genetic changes. Genetic changes are likely reversible only over a long time-scale. Effects on recruitment unclear, although shown in models. Given the current very healthy stock status, unlikely to be strongly negative	Jørgensen *et al.* (2007), Marshall and McAdam (2007), Enberg *et al.* (2009)
	Geographical distribution of spawning	Fluctuations well documented. Suggested causes involve changes in temperature, size of the individual fish, or both. Effect on recruitment is unknown	Sundby and Nakken (2008), Opdal *et al.* (2008, 2011)
	Date of spawning	Variation at any location is small, but change in average spawning latitude may also affect date. Still, strong effect on overall recruitment unlikely	Pedersen (1984), Otterå *et al.* (2006)
Egg	Quantity	Intuitively a good estimate of abundance also at future stages, depending on degree of later density-dependence, but analyses inconclusive	Mukhina *et al.* (2003)
	Quality, including size	Some quality features hard to quantify. Egg size from one individual decreases with batch number. Egg size tends to be reduced through the season. Shown in laboratory. Effect on interannual variation in recruitment unknown	Kjesbu *et al.* (1991), Solemdal *et al.* (1995)
	Specific gravity	Important, as it affects advection and dispersion. Likely to lead to differences in survival in eggs from different females. Effect on interannual variation in recruitment unknown	Kjesbu *et al.* (1992), Jung *et al.* (2012)
	Temperature	Pronounced effect on time to hatching. Likely a strong source of interannual variation in early life survival	Ellertsen *et al.* (1987)
	Advection and dispersal	Likely a strong source of interannual variation in early life survival. Field data to prove this difficult to obtain. Investigations done by numerical modelling	Vikebø *et al.* (2005, 2007)
	Predation	Important. The above factors all, to some degree, act through influencing predation	Melle (1985)
Larvae-pelagic juvenile	Temperature	Pronounced effect on survival, e.g. through affecting growth rates. Effects at population level documented. Likely a strong source of interannual variation in early life survival	Ellertsen *et al.* (1987), Ottersen and Loeng (2000), Folkvord (2005)
	Advection and dispersal	Likely a strong source of interannual variation in early life survival. Field data to prove this difficult. Investigations done by numerical modelling	Fiksen *et al.* (2007)
	Light	Documented to affect feeding success, duration, and rate of food searching. Source of difference in growth rate between stocks. Effects on interannual differences in BS cod not documented. UV also a potential source of variability, but effects on interannual differences in survival of BS cod not documented	Kristiansen *et al.* (2011)

	Wind-induced turbulence	Mechanism of turbulence affecting contact rate with prey well documented, but degree and even sign of effect still open for discussion. Field-based evidence exists, but hard to document effect at population level	Sundby and Fossum (1990), MacKenzie and Kiørboe (1995), Browman (1996), Sundby (1997)
	Prey	Good knowledge of what the larvae and pelagic juveniles eat. It is also known that the diet composition may fluctuate from year to year, but less about to what extent this influences variability in survival and thus recruitment. The match–mismatch hypothesis addresses temporal (and also spatial) overlap with prey	Sysoeva (1964), Ellertsen *et al.* (1980), Tilseth (1984), Cushing (1990), Karamushko and Karamushko (1995), Durant *et al.* (2007)
	Predation	Several species are identified as predators on BS cod eggs and larvae. Little is known about to what extent predation causes interannual variability in survival	Melle (1985)
Demersal juvenile-recruitment at age 3	Prey	Good knowledge of what they eat and that they shift towards being more generalists. Abundance of Euphausids (the main food item) is one of factors determining survival	Ponomarenko (1965, 1973b, 1984), Dalpadado and Bogstad (2004)
	Predation	Cannibalism is recognized as an important source of interannual variability in survival. Increasing cannibalism when low capelin abundance Little quantitative knowledge on effects by other predators	Bogstad *et al.* (1994), Hjermann *et al.* (2007), Yaragina *et al.* (2009), Haug *et al.* (2011)
	Geographical distribution and ambient temperature	Spatial differences in temperature important for growth. Distribution affects predation, prey availability, and temperature. Spatial patterns in survival have been pointed to and some evidence for interannual differences in survival patterns found	Ottersen *et al.* (1998), Ciannelli *et al.* (2007), Eriksen *et al.* (2011)

in that there are no predators in the former, thus allowing for survival to age 1 of juveniles that would not survive in nature (e.g. more weak/small and inexperienced individuals).

Paternal effects

Paternity has been shown to have a strong influence on many parameters, including fertilization success, hatching success, and cumulative larval mortality (Kroll *et al.*, 2013). Since paternal effects to little degree have been examined for BS cod, this paragraph draws upon results from experimental studies on Northwest Atlantic cod, which may be relevant also for BS cod. Experiments on gametes of both male and female cod showed that the paternal variance components, as well as the maternal, were significant for fertilization success (Butts *et al.*, 2009). By integrating population data and experimental findings on captive cod, Trippel (2003) generated a time-series of estimates of viable sperm production for cod off Newfoundland and Labrador (Division 2J3KL). Trippel (2003) found that marginally more of the variance in recruitment for this stock could be explained by viable sperm production when compared with SSB. Furthermore, due to the faster depletion of the testes in young, relative to old cod, stocks with pronounced juvenation may experience a shortening of the spawning season relative to the historical average (Trippel and Morgan, 1994; Nash *et al.*, 2008).

Male/female ratio

Lifespan and age at maturation differ systematically between male and female BS cod; males typically maturing ∼1 year younger and 10 cm smaller (Ajiad *et al.*, 1999). This and that males on average also die younger than females, leads to the gender ratio differing according to age or size groups (Yaragina *et al.*, 2011). On average, males are in majority among mature BS cod up to 10 years, while the oldest and largest fish are predominantly females (Ponomarenko and Yaragina, 1995; Ajiad *et al.*, 1999; Marshall *et al.*, 2006). However, the ratio of females/males in the BS cod spawning population exhibits pronounced fluctuations over time and varied between 24 and 68% over the period 1946–2001. For example, quite low ratios were recorded in the late 1960s and late 1980s (Yaragina *et al.*, 2011). It is to be expected that such fluctuations may significantly influence the numbers of eggs actually produced. Thus, this is a factor that may introduce a bias in the SSB estimates of productivity relative to the TEP.

Skipped spawning

SSB does not always adequately represent TEP. One factor that could significantly impact the number of eggs actually produced is skipped spawning, the failure of iteroparous spawners (animals capable of repeated spawning, like cod) to use each spawning opportunity after initial sexual maturation (Bull and Shine, 1979; Jørgensen *et al.*, 2006). Rideout *et al.* (2005) reviewed the physiology and histology of skipped spawning for fish. They state that methodological problems in identifying the post-mature non-reproductive state, especially related to the time of sampling, have led fisheries science to underestimate the frequency of skipped spawning and thus also its importance for recruitment (Rideout *et al.*, 2005). The occurrence of skipped spawning is particularly frequent for long-lived migratory fish with large energetic demands for reproduction (Secor, 2008), a description that BS cod fit well into. When some portion of a fish population skips spawning, the theoretical annual egg production of the population is reduced. Skipped spawning has been reported for a large fraction (up to 30–40%) of the mature fish for several cod populations in the Northwest Atlantic (Walsh

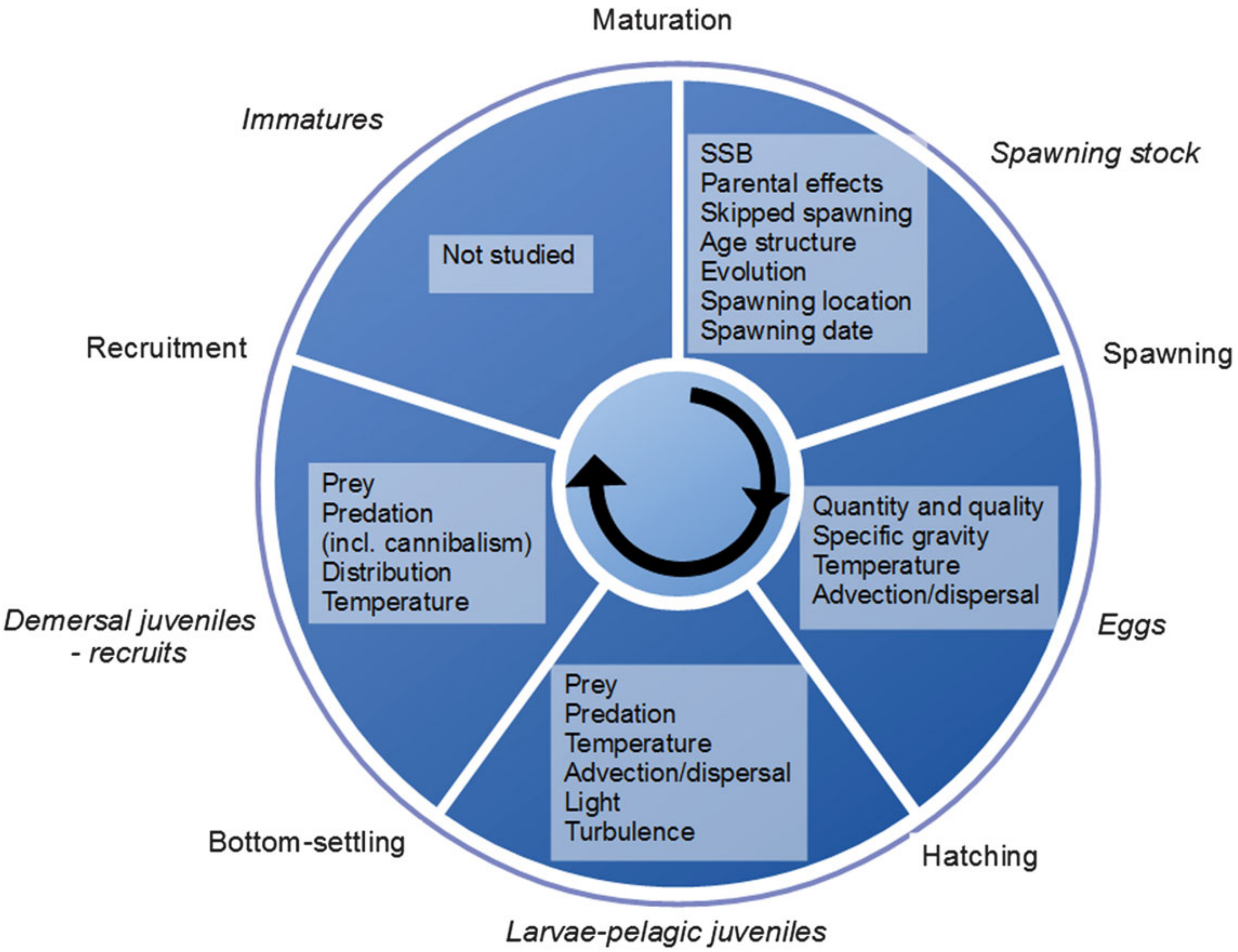

Figure 2. Conceptual Paulik diagram (Paulik, 1973) for Barents Sea cod. Factors determining survival from one stage to the next are shown in the sector between them. The diagram should be read clockwise, starting from the spawning stock, thus following the development life cycle.

et al., 1986; Burton *et al.*, 1997; Rideout *et al.*, 2000). The BS cod population exhibits intermediate levels of skipped spawning. At the population level, the percentage of "skippers" among the mature fish varied annually between 4 and 21% during 1984–2006 (Yaragina, 2010). Skjæraasen *et al.* (2012) found that "skippers" were approximately equally abundant as spawning females in 2008. In the total population that year, 24% of the females between 60 and 100 cm skipped spawning, 25% were developing oocytes, and 51% were immature.

There are two main modes of skipping observed to any extent in teleosts in the wild. *Resting* skippers do not start oocyte development, while *reabsorbing* skippers start oocyte development but later go through mass atresia (reabsorbing of eggs). It should be noted that almost every individual cod reabsorbs a minor fraction of her eggs. Skjæraasen *et al.* (2012) point out that BS cod skippers to a large extent employ the resting strategy. Individuals utilizing this strategy avoid any energetic costs connected to migration (or massive atresia) by remaining on the feeding grounds in the Barents Sea when spawners undertake their long southward migration. Experimental work on captive fish has demonstrated that skipped spawning indeed is highly influenced by individual energy reserves (Kjesbu *et al.*, 1998; Skjæraasen *et al.*, 2009, 2012). An example of this is that many BS cod were found to have skipped spawning in the late 1980s, likely due to their low condition after the collapse of the capelin (*Mallotus villosus*) stock (Marshall *et al.*, 1998). Since the degree of skipped spawning in BS cod seems to vary significantly between years, it could be an underlying factor causing some of the otherwise unexplained recruitment variation (Skjæraasen *et al.*, 2012).

Spawning stock age structure

Many authors have expressed concern about the loss of old and large individuals as a consequence of the worldwide intense exploitation of many marine fish populations that has taken place during the recent decades (Law, 1991, 2000; Longhurst, 2002). Such a worry was also voiced regarding the BS cod many years ago by Sætersdal and Hylen (1964) (cited by Nakken, 1994) and somewhat later by Borisov (1978) and Ponomarenko (1984) and is especially related to the consequences of the large-scale size-selective trawl fishery taking place in the Barents Sea from the 1950s onwards. In particular, it has been suggested that fishery-induced juvenation of spawners may impair recruitment (Beamish *et al.*, 2006), also for BS cod (Ponomarenko, 1973a). Further, it has been argued that the reported loss of age diversity among spawners may have negative consequences for recruitment to the cod stocks around Iceland (Marteinsdottir and Thorarinsson, 1998) and on Georges Bank (O'Brien *et al.*, 2003).

Thus, as a consequence of decades of trawl fisheries, we might expect BS cod recruitment to have been seriously impaired towards the end of the 20th century. Indeed, the spawning stock of BS cod did become younger, dominated by fewer age classes and with a larger proportion of first-time spawners (Ottersen, 2008). However, a statistical inspection of the relations between BS cod recruitment or survival (recruitment/SSB) and variables related to spawner age and spawning experience showed no clear association (Ottersen, 2008). Further, the low fishing pressure in recent years has, together with strong year classes in 2004 and 2005, caused the spawning stock to grow to the highest level seen in the time-series, and the age diversity in the stock has increased considerably during the last 5 years (ICES, 2013).

Fisheries-induced evolution

It has been suggested that heavy fishing pressure in general and fishing targeting large individuals in particular may have caused genetic changes in many harvested fish populations, including BS cod (Heino, 1998; Jørgensen *et al.*, 2007). If these changes affect early life history traits, e.g. by reducing egg volume or larval size at hatch, they may have considerable consequences for recruitment (Walsh *et al.*, 2006). Through laboratory experiments on Atlantic silverside (*Menidia menidia*), Conover and Munch (2002) showed that size-selective harvesting can select for genotypes with slower or faster growth rates depending on whether large or small individuals are selectively removed. Thus, size-selective fishery has the potential to lead to rapid evolutionary response. However, after the extremely high experimental selection was relaxed, the changes reported by Conover and Munch (2002) were reversed (Conover *et al.*, 2009). Also, in real fisheries, selection is not knife-edge and it acts on size rather than directly on growth rate (i.e. it can include slow-growing old fish as well as fast-growing young fish); therefore, the rates observed in such experiments are not necessarily representative (Andersen and Brander, 2009).

Although size-selective harvesting clearly may cause pronounced changes in life history of exploited species, it often remains unclear whether the observed changes have a genetic basis or are a result of phenotypic plasticity (Law, 2000; Fenberg and Roy, 2008). To separate evolutionary responses to fishing from phenotypic plasticity, probabilistic reaction norms for age and size at maturation may be used (PMRN; Olsen *et al.*, 2004; Dieckmann and Heino, 2007). For a cohort, the PMRN describes the maturation probability at each age and length combination. If there is no change over time in cohort-specific PMRNs, then it is generally inferred that there has been no evolution; if the PMRN midpoints decline in time then fisheries-induced evolution is diagnosed (Marshall and McAdam, 2007). However, when testing the method on BS cod, Marshall and McAdam (2007) found that the evidence for an evolutionary change was inconclusive. Maturation trends could be interpreted as showing either a strong environmental effect, no genetic effect, or a strong genetic effect. On this basis, Marshall and McAdam (2007) concluded that a more integrated view of maturation, incorporating key aspects of the physiological processes that culminate in maturation, is required to avoid incorrect inferences about the underlying causes of earlier maturation. Still, modelling results by Eikeset (2010) indicates that the observed historical changes in age and length at maturation of BS cod could be best explained by jointly considering both ecological and evolutionary effects. Also, Enberg *et al.* (2009) employed an individual-based evolutionary model parameterized for a BS cod-like fish to investigate a stock's response to fishing followed by a harvest moratorium. The model allows evolution of life history processes including maturation, reproduction, and growth while also incorporating environmental variability, phenotypic plasticity, and density-dependent feedbacks. Enberg *et al.* (2009) found that recruitment was one of the stock characteristics substantially affected by fisheries-induced evolution.

Spawning location and timing

Spawning of the BS cod takes place in patchy areas along the 1500 km long coast of mid and northern Norway, with Lofoten/Vesterålen as the core spawning region (Figure 3). Already Hjort (1914) noted that spawning was restricted to banks near the coast. The hydrographical conditions on and around the spawning banks are highly dynamic, but with longer term dominating flow directions following the bottom topography towards the north. The area is influenced by Atlantic and coastal currents as well as local freshwater run-off. Thus, future recruitment may be influenced by variability in hydrography, wind, and tidal conditions at the spawning sites. At which sites spawning actually takes place varies both in the short and long term. Shifts in spawning locations might take place at different spatial scales and from year to year, within a single spawning season and even from day to day in response to the physical forcing factors given above, which can alter the position of the thermocline where BS cod spawning usually takes place (Ellertsen *et al.*, 1981; Sundby and Solemdal, 1984).

At the decadal time-scale, a pattern of increase in the proportion of spawners caught north of the Lofoten archipelago (Figure 3) during the period 1910–1940 and more recently from the early 1980s until the early 2000s was pointed to by Sundby and Nakken (2008) and Opdal (2010). There are two main proposed causes for this distributional shift. Sundby and Nakken (2008), based upon correlations between a roe index acting as a proxy for spawning location and sea temperatures in the southern Barents Sea, suggested that the northward shifts were caused by rising temperatures. Alternatively, the migration pattern of BS cod may have been changed by a size-selective trawl fishery in the Barents Sea reducing the average size of the fish and thus the migratory capacity of the stock (Jørgensen *et al.*, 2008; Opdal, 2010). Opdal (2010) further suggested that the observed abandonment of the more southerly spawning grounds, leading to a pronounced reduction in the latitudinal range of offspring nursery areas, possibly may have made recruitment processes less resilient towards adverse climatic conditions. Note, however, that the two suggested mechanisms are not mutually exclusive.

Latitudinal shifts in spawning location may also influence the average date of spawning, with a tendency for delayed spawning at the northern sites (Sundby and Bratland, 1987). Spawning date may again be important for recruitment, especially since it may affect the probability of the cod larvae to find sufficient prey. Otterå *et al.* (2006) presented compelling evidence for the spawning time in cod having a genetic component. They showed that time of peak spawning differed with up to 1 month between Norwegian coastal cod broodstocks originating from different regions along the Norwegian coast and that the differences persisted also during the second spawning season after capture. Even so, within a region, at least in Lofoten/Vesterålen, the timing of spawning varies little from year to year. Spawning starts at the beginning of March, peaks in the first week of April, and terminates at the beginning of May (Sundby and Bratland, 1987; Sundby and Nakken, 2008). This stability in spawning period between years has been interpreted as an indication that the seasonal light cycle is the main trigger for spawning (Sundby and Nakken, 2008). If this is the case, interannual variability in recruitment should not be expected to be connected to the time of spawning (this having

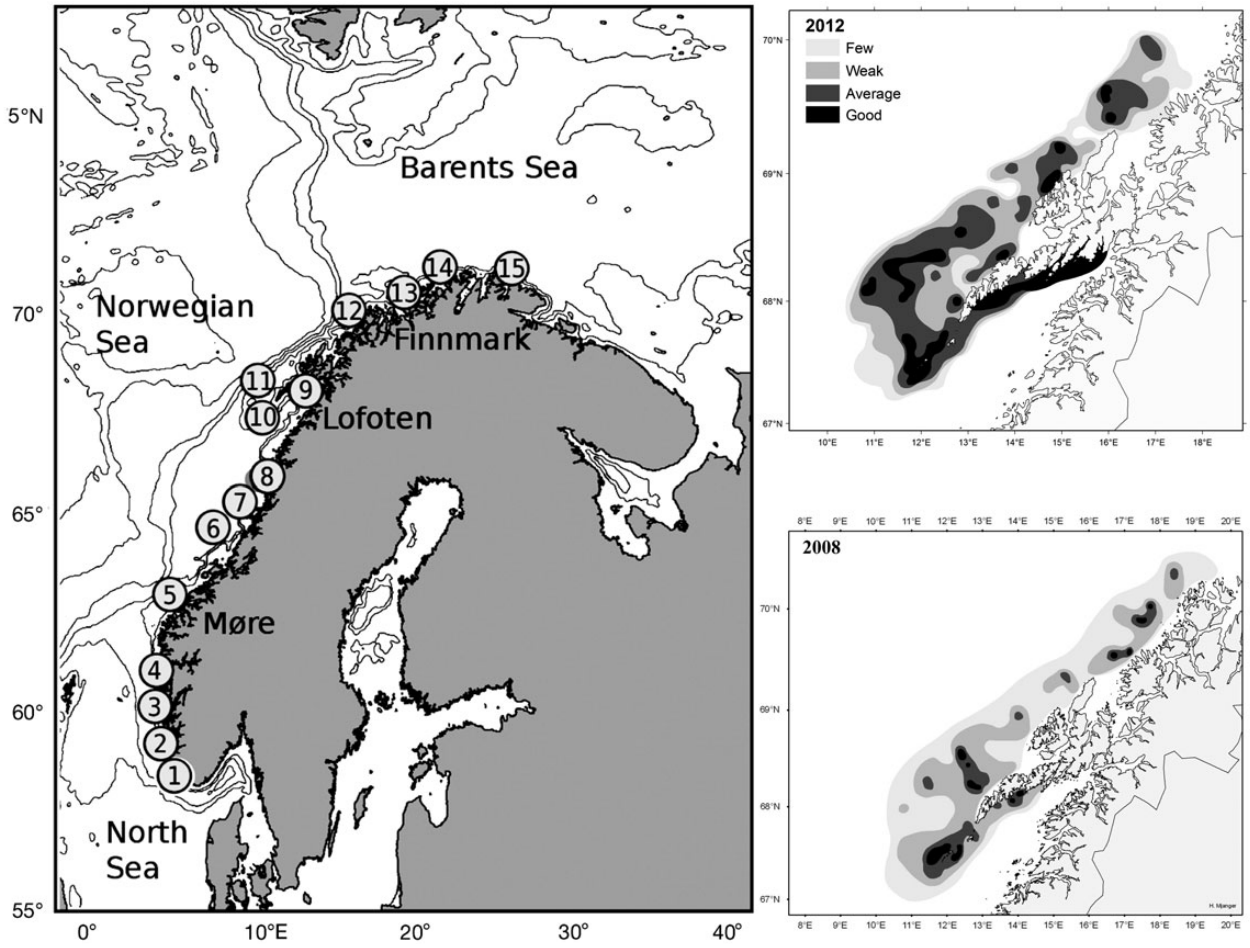

Figure 3. (Left panel) Location of present day and historical BS cod spawning grounds along the Norwegian coast, from south to north: (1) Vest-Agder, (2) Rogaland, (3) Hordaland, (4) Sogn, (5) Buagrunnen (Møre), (6) Yttergrunnen, (7) Vikna, (8) Vega, (9) Vestfjorden, (10) Røstbanken, (11) Moskenesgrunnen, (12) Malangsgrunnen, (13) Breivikbotn (West-Finnmark), (14) Central-Finnmark, (15) East-Finnmark. Bottom topography is indicated by 100 m depth contours. (Right panels) Distribution and abundance of spawning fish in the Lofoten/Vesterålen area 16 March – 8 April 2012 (upper right panel) and 17 March – 5 April 2008 (lower right panel). Map in the left panel from Opdal *et al.* (2011), upper right by Karen Gjertsen, and lower right by Hildegunn Mjanger, both Institute of Marine Research, Norway. Scale for acoustic density s_A (backscattering area, m^2 nm^{-2}) used in maps: few: $10 < s_A < 50$, weak: $50 < s_A < 250$, average: $250 < s_A < 1250$, high $s_A > 1250$.

only minor variability), but rather to time of spring bloom. Indeed, there is substantial interannual variability in spring bloom date at a given location (Sakshaug *et al.*, 2009). Further, there is also a latitudinal gradient. Estimates of time of spring phytoplankton bloom based on remote sensing data (SEAWIFS, oceancolor.gsfc.nasa.gov) suggest an average delay of 37 d from Møre (60–62°N) to Lofoten (68–70°N) (Figure 3; Vikebø *et al.*, 2012). This is consistent with the observed delay in time of spawning of BS cod with increasing latitude (Sundby and Bratland, 1987).

Eggs

Hjort (1914) reflected that "The actual quantity of eggs spawned is not a factor in itself sufficient to determine the numerical value of a year class", as the 1904 year class turned out strong while the quantity of roe taken by fishery was small. Thus, other factors, including aspects of the egg stage beyond pure abundance, should also be considered. Table 2 gives an overview of properties and mechanisms suggested to impose interannual variability in survival of BS cod per stage.

Quantity, size, and quality

Atlantic cod is a multiple batch-spawner. In natural conditions, 3–8 batches per female have been observed within a single spawning season (Sorokin, 1957), in laboratory conditions, up to 20 batches (Kjesbu, 1989). The experimental study by Kjesbu (1989) further found that the amount of eggs released in each batch rose from the start of spawning (60–70 thousand eggs) to a maximum (300–310 thousand eggs) in the 10–13th batch, and then decreased again.

Egg quality or viability may be hard to define, but fertilization rates, egg survival, and larval features could be suggested as measures (Lambert *et al.*, 2003 and references therein). One quantifiable characteristic is egg size. The size of cod eggs varies significantly during the overall spawning period, generally being reduced through the season (Sivertsen, 1935; Solemdal, 1970; Solemdal and Sundby, 1981). This can partly be explained by the fact that small fish having smaller eggs (as mentioned under the "Maternal effects" section) are the latest to spawn, and partly by the mean egg size from a single female becoming progressively smaller with increasing egg batches (Kjesbu, 1989; Solemdal *et al.*, 1992; Marteinsdottir and Steinarsson, 1998; Trippel, 1998).

While fertilization rate does not seem to be influenced by the size of eggs (Solemdal *et al.*, 1992), larger egg size tends to lead to larger larvae (Trippel, 1998) and increased survival of eggs (hatching success; Solemdal *et al.*, 1995) and yolk-sac larvae (Nissling *et al.*, 1998), although the latter study found no effect of egg size on viability up until hatching. This is of particular interest to us since large larvae have been suggested by both field studies (Meekan and Fortier, 1996) and theory (Houde, 1987) to have increased viability due to better ability to utilize a broad food spectrum and to avoid predators. If extrapolating to the population level, this "bigger is better" argument, other factors unchanged, should lead to a year-class with larger than average eggs to ultimately have higher than average abundance at recruitment. However, this may be a bit too simplistic, as a trade-off between egg size and abundance is to be expected. Winemiller and Rose (1993) found by a simulation model that a fixed amount of reproductive effort generally should be partitioned into many small offspring in resource-rich habitats or into a few large offspring in resource-poor habitats. Further, contrary to what expected, Litvak and Leggett (1992) found by combined mesocosm and microcosm experiments that larger capelin larvae experienced greater mortality due to predation.

Specific gravity

Knowledge of the vertical distribution of fish eggs and larvae is crucial for understanding transport patterns and potential survival (Jung, 2012). The vertical distribution is determined by interaction between biological (egg density and size) and physical (water density, viscosity, turbulence) factors (Sundby, 1991; Jung, 2012). Egg buoyancy, i.e. the ability of the eggs to float naturally in seawater, is defined as the difference in specific gravity between the ambient water and the egg. The different populations of Atlantic cod seem to have surprisingly similar ranges of egg specific gravity and egg size, except in the brackish Baltic (Jung, 2012). Further, a negative trend, although not statistically significant, was found between egg specific gravity and total length of Norwegian coastal cod females by Jung *et al.* (2012). Finally, the variability of specific gravity was found to be greater at the individual level than between fish from different populations of Norwegian coastal cod (Jung *et al.*, 2012). If we extrapolate this latter finding, it may point towards quite large differences in survival probability of eggs from different females of BS cod, based upon the influence of specific gravity of eggs on their vertical positioning and hence, their drift pattern (e.g., Opdal *et al.*, 2011; Langangen *et al.*, 2014).

Temperature effect on duration of egg stage and survival

Buckley *et al.* (2000) found that low-temperature incubation of Atlantic cod (and haddock) eggs from a broodstock in captivity extended the embryonic period substantially. Atlantic cod embryos hatched at temperatures as low as −1°C, extended the embryonic period to 59 d. At 8°C, Atlantic cod (and haddock) embryos hatched in 11–12 days. To determine if extending the embryo incubation time by using low temperatures had a detrimental effect, embryos were incubated through hatch at either 1 or 0°C, and the larvae from both groups reared at 6°C. Growth and early survival of larvae were similar between treatments (Buckley *et al.*, 2000). Furthermore, temperature also affects the number of myotomes and vertebrae, both in cod (Hall and Johnston, 2003) and other species (Hempel and Blaxter, 1961; Jobling, 2012).

Based on field observations in Lofoten in 1983–1985, Ellertsen *et al.* (1987) found that the duration of BS cod's incubation period was 14 days shorter in the warmest vs. the coldest year. Langangen *et al.* (2014) quantified the importance of temperature-driven variability in egg stage duration for the cumulative survival of BS cod eggs. At higher temperature, egg stage duration is shorter and cumulative survival higher (all else being equal). From a 35-yr observational dataset on cod eggs at different developmental stages, they estimated that the instantaneous egg mortality rate was on average around $0.17\ \mathrm{d}^{-1}$, resulting in a cumulative survival of around 3% for a 20-d egg stage duration. The ambient temperature of the eggs varied interannually with ± 1.1°C and the egg stage duration with ± 3.3 d, according to coupled biological-oceanographic model simulations. In effect, the cumulative survival was estimated to be three times higher in an exceptionally warm year (anomaly +1.1°C) compared with an exceptionally cold year (anomaly −1.1°C) at a given instantaneous mortality rate of $0.17\ \mathrm{d}^{-1}$. The analysis of the observation data suggested that the instantaneous mortality rate also varied among years, however, leading to up to ninefold difference in cumulative egg stage survival among years (Langangen *et al.*, 2014). In comparison, cumulative survival through the larval stages (a period of 2 months or more) has been reported to vary 68-fold among years (Sundby *et al.*, 1989).

Advection and dispersal

Specific gravity of eggs (discussed above) and the level of mixing in the ambient water column determine the vertical positioning of eggs. For BS cod, this has been demonstrated in the field under various climatic conditions and a theoretical framework has been established (e.g. Sundby, 1991). Early work points to the distribution of eggs (and later larvae) being influenced by the intensity of the flows at the boundary between the Barents and Norwegian Seas and the predominating winds during their drift period (Kislyakov, 1964; Corlett, 1965; Tereshchenko, 1980; Dvinina and Mukhina, 1984). Kislyakov (1964) suggested that the distribution of cod eggs in the surface layer was significantly influenced by the crest (ridge) of the increased level of relatively fresh water that extends northwards from the Norwegian coast. This idea was carried on by Tereshchenko (1980) and Mukhina *et al.* (1987) who proposed that the more pronounced the crest was, the farther northwards of the Lofoten banks the cod eggs were transported, and the larger was the area of their distribution. Furthermore, Tereshchenko (1980) points to atmospheric circulation affecting the direction of eggs and larvae drift. The difference in mean air pressure in March–May between Bear Island and Jan Mayen (Figure 1) was taken as an index of predominant air mass transport, with positive values indicating prevailing southerly winds and hence the intensity of the drift of cod eggs to the Bear Island-Svalbard area (Tereshchenko, 1980).

In the past, multiple measurements of egg densities and sizes along with density profiles of the ambient waters revealed a large number of eggs near the surface, while decaying near exponentially with depth (Solemdal and Sundby, 1981). Hence, while the individual egg is being moved up and down in the water column according to its buoyancy and the level of mixing in the water surrounding it, the average vertical distribution of eggs are near-stationary as long as the mixing of the water column, e.g. due to winds, remain unchanged. However, under various wind regimes, the average vertical egg profile changes, becoming deeper during strong mixing and more shallow during weak mixing. This knowledge has also been used to quantify the eddy diffusivity coefficients based on density measurements of eggs and the water, size of eggs, and vertical distribution (Sundby, 1983). Still, it has been difficult to infer the dispersal effects of varying vertical positioning by field measurements. There have been a number of studies where drifter buoys have been released at sea in the area of drifting BS cod eggs, both individually and in pairs, but these have typically all been drifting at the same depths, either as near-surface (~10–20 m) drogues or surface floats (e.g. Sætre, 1999; Koszalka *et al.*, 2011; Röhrs *et al.*, 2012). However, the introduction of individual-based models (IBMs) made available quantitative measures of how the behaviour and state of individual embryo and larva can be related to population level distributions (Vikebø *et al.*, 2005, 2007). An IBM is a model that predicts population level outcomes by integrating across individuals with various traits, which respond to environmental exposure according to known processes (Grimm and Railsback, 2005). An IBM of pelagic free drifting early life stages of BS cod includes a simple Lagrangian particle-tracking model, where particles are introduced to the habitat of BS cod at various sites and times and are dispersed according to the spatio-temporally varying three-dimensional currents. By discretizing the functional relationship between buoyancies and mixing (e.g. Thygesen and Ådlandsvik, 2007), one may utilize a particle-tracking model for horizontal dispersal according to predicted currents, while at the same time accounting for the dynamic vertical positioning of the individuals (e.g. Myksvoll *et al.*, 2011; Opdal *et al.*, 2011; Langangen *et al.*, 2014). The ability to accurately describe the dynamical vertical positioning of individual eggs is important because it allows studies of how a range of spatial forces such as UVR-exposure, dispersal, and exposure to pollutants possibly affect recruitment.

Progressive vector diagrams from Acoustic Doppler Current Profiler measurements (Skagseth *et al.*, 2011) clearly indicate that eggs floating at different depths will disperse differently. However, systematic investigation of this has only been carried out numerically. While dynamic vertical positioning of eggs is well understood and properly incorporated in numerical models addressing early life history of BS cod, there are a number of additional challenges. Direct measurements of eddy diffusivities reveal a high degree of variability. Eddy diffusivities are parameterized in numerical models (see Large, 1998, for a review of different schemes) but are typically not well captured near the surface (J. Röhrs, pers. comm.). Another major challenge of the numerical studies investigating BS cod egg dispersal is the trade-off between spatial resolution and size of model domain. Most BS cod spawning areas are near the rugged coast. The computational resources available today are limited when considering the need for high spatial resolution and the wide-spread spawning grounds. As a result, the available spatial resolution of the ocean model smoothes near-coast circulation and introduces errors in near-coast dispersal. As soon as the eggs are more dispersed, and on average displaced farther off the coastline, this problem becomes less severe. Myksvoll *et al.* (2013a) show how sensitive near-coast transportation is for the fate of the offspring. In most previous numerical studies of early stages of BS cod, the larval stage has been the focus and the dispersal of eggs has been a way to predict the spatio-temporal distribution of first-feeding larvae based on knowledge of the spawning grounds and the circulation.

Larvae and pelagic juveniles (0-group)

During their pelagic drift phase, larvae and later juvenile BS cod are faced with challenges involving spatially and temporally varying temperatures, advection and dispersal, light conditions, degree of turbulence or stability, prey availability, and predation. Each of these topics are discussed in the following paragraphs and briefly summarized in Table 2.

Temperature

The growth and survival of early stages of BS cod have in many papers been shown to be influenced by sea temperatures. Comparisons of experimentally derived growth rates of cod larvae and field-based growth estimates suggest that surviving cod larvae in the sea typically grow at rates close to their size- and temperature-dependent capacity (Folkvord, 2005). This demonstrates that climatic influences may strongly affect the year-to-year variations in growth of cod during their early life history owing to their markedly temperature-dependent growth potential. Thus, in the Barents Sea, warm conditions (relatively speaking), associated with increased inflow of Atlantic water (Loeng, 1991; Ottersen and Stenseth, 2001), are commonly considered to be necessary, but not sufficient for high survival and ultimately a strong cod year class (Sætersdal and Loeng, 1987; Ottersen and Loeng, 2000). Survival increases in warm years due to both direct temperature effects (higher growth rates, Ottersen and Loeng, 2000) and indirect temperature effects (greater food availability, Sysoeva and Degtereva, 1965). We will in the following show several examples in support of this.

The results of the spatio-temporal statistical analysis of Stige *et al.* (2010) indicated positive effects of ambient temperature on growth to the age-0 stage for BS cod. Further, Ottersen and Loeng (2000) showed that growth and survival to the age-0 stage of BS cod (as well as haddock and herring in the Barents Sea) was positively correlated with temperature, and that the combination of abundance and mean length at the age-0 stage was a good predictor of recruitment at age 3. Such links between growth and survival are not uncommon and fit into the "bigger is better" concept discussed under "the egg stage".

Also the distribution of BS cod larvae seems to be affected by temperature, in warm periods they are spread over a wider temperature range, larger area, and further downstream. This is related to (i) higher abundance of spawners, (ii) an increase in ocean transport, (iii) higher overall survival (possibly because of better food availability and/or escape from predation), and (iv) a change in the spatial survival pattern, likely caused by changes in spatial distribution of predators or prey (Hidalgo *et al.*, 2012). Eriksen *et al.* (2012) analysed the non-linear associations between spatial and temporal variations in temperature and abundance and length of age-0 BS cod. Cod density and length were greatest in the temperature range 4.4–8.0°C, indicating that an increase in temperature to above this possibly optimal range may not lead to further increases in cod density and length.

Advection and dispersal

What may be called Hjort's second hypothesis relates to "another point which might be considered as possibly exerting some influence upon the mortality of fish in the early stages, viz, the passive movement of the larvae with the currents" and further "It would be especially desirable to ascertain the extent of such movement, and how far the young fry are able to return, of their own volition, to such localities as offer favourable conditions for their further growth" (Hjort, 1914, 1926). This idea of "aberrant drift" (Houde, 2008) laid the foundation for further developed hypotheses with a focus on larval distribution. The "member-vagrant" hypothesis focuses on the role of retentive hydrographic structures, which result in limited dispersal of early life history stages (Sinclair, 1988;

Sinclair and Iles, 1989; Werner and Quinlan, 2002). The "migration triangle" hypothesis takes a somewhat different aspect. Here the focus is on spatially separate adult feeding grounds, spawning grounds, and juvenile nursery between which fish must migrate to close their life cycle. Successful larvae are advected from the spawning to the favourable nursery grounds, the surviving juveniles and adults later move to particular feeding grounds, and adult spawners migrate contranatant to return to the spawning grounds (Harden-Jones, 1968; Cushing, 1975; Secor, 2002). DeYoung *et al.* (2010) point to BS cod as a stock that fits such a model of spatial migration linked to ontogenetic development.

Annual surveys, designed to measure the abundance and distribution of BS cod, are typically carried out for the egg stage and the pre-settlement 0-group fish. These surveys provide interesting knowledge on interannual differences in features relevant to recruitment. They do not, however, provide information on individual dispersal trajectories and corresponding environmental exposure. Such information is highly relevant, e.g. in the context of the hypotheses above, and may be gained from IBMs of early stages of fish coupled to ocean models (Miller, 2007). As noted under *The egg stage: Advection and dispersal*, an early life history IBM for BS cod includes a simple particle-tracking model, which is extended with modules considering key processes such as growth, survival, and behaviour according to the current knowledge level, and individuals' traits. A thorough description of an early life history IBM of BS cod is given in Kristiansen *et al.* (2007), including mechanistic feeding and growth, and survival dependent on size, food, and predators. Parameterizations of the different components of the model are collected from many laboratory experiments. Recent investigations of the effect of various behavioural traits on horizontal dispersal and environmental exposure include those of Vikebø *et al.* (2007) and Fiksen *et al.* (2007). Here, individual risk awareness or preferred horizontal swimming preferences significantly affected the subsequent environmental exposure and distribution. In general, the realism of an IBM approach to early life history of fish relies on the ability of the ocean model to capture relevant scales of ocean hydrography and dynamics, and the accuracy in the physiological and behavioural responses of the model fish.

A number of studies, where either simple particle-tracking models or advanced IBMs are coupled to ocean models, describe processes that either directly or indirectly affect dispersal, and thus also survival and potentially recruitment of BS cod. Hidalgo *et al.* (2012) combined numerical and statistical modelling in a novel approach. Drift of BS cod eggs from the spawning grounds to the early juvenile stage was computed by a particle-tracking model forced by current fields from an ocean model. By comparing the predicted and observed distributions of early juvenile BS cod for the same 6 years using a spatial generalized additive model, Hidalgo *et al.* (2012) quantified the effects of predictor variables potentially linked to survival. Results suggested differential effects of local temperature and spatial location on larval abundance dependent on the state of the North Atlantic Oscillation (NAO). This was hypothesized by Hidalgo *et al.* (2012) to be linked to differences in spatial overlap of the fish larvae and their prey. Vikebø *et al.* (2005) showed that a shallow drift of BS cod offspring results in dispersal farther from the coast and eventually also more into the central parts of the Barents Sea when compared with a deeper drift depth. This is also demonstrated by Vikebø *et al.* (2007), but here also short- vs. long-term trade-offs with respect to growth and survival are considered. An optimal vertical behaviour with respect to feeding and hiding from predators, given the limitations of the model setup, measured against long-term survival is suggested. A similar approach, but with an even more advanced IBM with respect to feeding and behavioural rules, and vertical prey and larval distributions from field, underlined the need for resolving feeding behaviour for modelling vertical behaviour of cod (Kristiansen *et al.*, 2009a).

Light

The effect of light intensity on swimming behaviour has implications for feeding success of fish larvae (Batty, 1987). In teleost larvae, total reliance on visual cues for feeding is common (Miner and Stein, 1993; Hart *et al.*, 1996). Feeding opportunities of larval cod are thus constrained by light. Hatching of BS cod occurs from late March to late May, a period when the number of daylight hours in their core distribution area increases from 11 to 17. Models suggest that larval BS cod experience lower growth if hatched early in the season (before mid-April) when the foraging hours are few (Kristiansen *et al.*, 2009b, 2011). In comparison, larval cod hatched in early May experience higher temperatures, better growth conditions, and are, due to increased daylength, less susceptible to prey limitation (Kristiansen *et al.*, 2009b).

Suthers and Sundby (1996) compared observed growth rate between BS and southwest Nova Scotia, Canada (4X), cod. They found that size-at-age of pelagic juvenile BS cod was approximately twice that of the 4X cod. Statistical analysis revealed that this difference could not be explained by temperature and prey biomass alone. Using the light intensity threshold for larval cod feeding, they estimated that there is 48% more time during May–July for visual feeding north of the 71°N latitude of northernmost Norway than at the 43°N of southwest Nova Scotia. Although genetic differences could be part of the explanation for the differences in size-at-age, the results pinpoint time available for feeding as a main factor (Suthers and Sundby, 1996). Helle (2000) found no diurnal trends in stomach fullness or degree of digestion of cod larvae in the Barents Sea, suggesting that feeding is continuous. Within the BS cod stock, the interannual north–south variability in spawning locations, described earlier, may in principle also affect time available for visual feeding for the larvae through differences in daylength. However, since the most southerly location with sizeable BS cod spawning is at 64°N and the northernmost is at 71°N, the potential difference is far less than between BS and 4X cod.

Light may affect early stages of BS cod in other ways than through visual feeding. It is well established that ultraviolet radiation (UVR, 280–400 nm) may harm aquatic organisms. In particular, UVR may potentially affect cod eggs. Eilertsen *et al.* (2007) simulated the UVR dose that eggs and larvae of cod receive during spring in Lofoten. They found that although there may be episodic events of UVR-induced mortality of cod eggs and larvae, the overall effect on year-class strength was insignificant. A study conducted by Skreslet *et al.* (2005) suggested that local UVR might even have a positive effect on the survival of BS cod eggs and larvae, possibly through UVR reducing the amount of harmful bacteria. In another study, modelling conditions representative of the Gulf of St Lawrence, Kuhn *et al.* (2000) found that cod embryos were insensitive to UVR.

Wind-induced turbulence

Early work on first-feeding BS cod larvae underlined that low winds were favourable for feeding success (Rollefsen, 1930; Tilseth, 1984).

The suggested mechanism was that high-density patches of prey was necessary and that increased winds created a more homogeneous vertical distribution of both cod larvae and their zooplankton prey, thus reducing accessibility of food to the larvae (Tilseth, 1984). These ideas are closely related to the "stable ocean" hypothesis of Lasker (1975, 1978), which focuses on the role of vertical stratification in concentrating prey for fish larvae (northern anchovies in the California current) at the pycnocline. A subsequent retrospective study on the same species concluded that the year-class-strength was highest in periods of weak winds (Peterman and Bradford, 1987).

Taking a different angle, theoretical work by Rothschild and Osborn (1988) demonstrated how turbulence potentially could increase the encounter rates between planktonic predators and their prey. The importance of small-scale turbulence to encounter rates was supported by a simulation study by MacKenzie and Leggett (1991). Several papers applying the Rothschild–Osborn theory to BS cod larva by field data were subsequently published. Sundby and Fossum (1990) pointed to wind-driven turbulence being an important feature of the mixed layer and that this is the habitat for BS cod from egg until the settling juvenile stage at 5–6 months of age. All low-speed predators are influenced by these processes, including cod larvae and those that prey on cod larvae. Therefore, small-scale turbulence and predator–prey contact rate is likely to be important regulatory mechanisms in the formation of BS cod year-class strength (Sundby and Fossum, 1990). Sundby (1997) argued that wind-induced turbulence strongly enhances the feeding rate of first-feeding cod larvae. Their feeding rate increased by a factor of ~7 with an increase in windspeed from 2 to 10 m s^{-1}. Further, model simulations show how the influence of turbulence-enhanced encounter rate decreases exponentially as the larvae grow, increase their swimming speed, and switch to larger prey of lower concentration (Sundby, 1995, 1997).

In concordance with Sundby (1995, 1997), MacKenzie *et al.* (1994) and MacKenzie and Kiørboe (1995) found, based upon experimental laboratory studies, that turbulence can have beneficial or detrimental effects on larval fish ingestion depending on the magnitude of the turbulence, resulting in a dome-shaped relationship. However, the latter mentioned papers placed emphasis on larval behaviour. The level of beneficial turbulence changes with larval size and too strong turbulence may move the prey outside a larva's perception area before a pursuit response is triggered. The reduction in pursuit success in highly turbulent environments negates the increase in encounter rate. Thus, a dome-shaped relationship was found where ingestion rates are maximal at intermediate rather than high levels of turbulence (MacKenzie *et al.*, 1994; MacKenzie and Kiørboe, 1995). We cannot go further into this discussion here. Instead, we refer to a special Comments Section in Marine Ecology Progress Series, which covers the main viewpoints on the turbulence issue, from the physics, fisheries ecology, and behavioural perspectives (Browman, 1996) and more recent papers by Galbraith *et al.* (2004) and Ruzicka and Gallager (2006).

Prey

BS cod larvae diet composition may fluctuate from year to year (Karamushko and Karamushko, 1995). This may again affect condition and even mortality, eventually influencing recruitment. The larvae switch from endogenous (yolk sac) to exogenous feeding 5–7 d after hatching. The first food of BS cod larvae is predominantly nauplii of copepods (B. Ellertsen, ex. Institute of Marine Research, Norway, pers. com). Large cells of phytoplankton, like *Thalassiosira hyalina*, *Peridinium depressum* (Wiborg, 1948; Ellertsen *et al.*, 1980), are also observed in larval guts, though their nutritional value is likely to be low due to the resistance to digestion. The diet of larger larvae mainly consists of copepodites of *Calanus finmarchicus* and also *Oithona similis, Evadne nordmanni* (Cladocera), appendicularians, and larvae of Bivalvia. In the diet of the largest larvae, euphausiid juveniles may dominate (Manteyfel, 1941; Degtereva, 1964, 1970, 1979; Sysoeva, 1964, 1973; Pedersen and Fossheim, 2008). Larvae are sporadic feeders, pausing between feeding to digest food (Tilseth, 1984). The diets of cod and herring larvae suggest that they may compete for the same food (Pedersen and Fossheim, 2008).

The energetically minimum necessary daily ration of larval BS cod has been estimated to be in the range 16.0–24.6% of body weight, with a tendency to decrease with increasing larval size. Actually observed mean rations for cod larvae in the Norwegian and Barents Sea in 1983–1985 varied strongly, with a range of 12.7–55.0%. This means that the observed rations in some cases were higher and in some cases lower than the theoretically minimal required ones (Karamushko and Karamushko, 1995). Dalpadado *et al.* (2009) found that *C. finmarchicus* and *Thysanoessa inermis* were the main prey of 0-group BS cod and haddock in August–September. The feeding areas and prey of 0-group cod and haddock overlapped, implying that competition for food may occur between the two species. However, haddock seems to prefer smaller and less mobile prey, such as *Limacina* and appendicularians. As 0-group BS cod increase in size, there is a shift in diet, from small copepods towards larger prey such as krill and fish (Dalpadado *et al.*, 2009).

Observations of prey availability for BS cod larvae are scarce and typically only available at a few stations and limited periods (T. Kristiansen, pers. comm.). Most studies involving an egg and larval IBM of BS cod do therefore not account for spatio-temporal variability in prey availability (but see Kristiansen *et al.*, 2009b). This limits the possibility of linking early life history of BS cod to recruitment variability. Kristiansen *et al.* (2009b) utilized modelled spatio-temporal varying abundance of stage-dependent *C. finmarchicus* as prey availability for cod larvae of different sizes at different locations and investigated the importance of turbulence-enhanced feeding when prey concentrations were low. However, as of yet, there are no published IBM simulations of BS larvae that drift through a time-varying modelled prey field as has been done for North Sea cod by Daewel *et al.* (2011).

Predation on eggs and pelagic larvae

There are few studies of predation on BS cod eggs and pelagic larvae. An overview is given in Pálsson (1994), who identifies both invertebrates (Medusae, ctenophores, crustaceans, chaetognaths) and fish as predators on eggs and larvae. Melle (1985) found that both herring, ctenophora, and Medusae ate cod eggs and larvae in the Lofoten area. Herring was identified as a heavy predator. However, the spatial distribution of herring in most years only has a limited overlap with the cod egg distribution (Holst *et al.*, 2002). Thus, the population level effect of herring (and other fish) predation on BS cod eggs and larvae is probably small, unlike in the Baltic where predation by sprat on cod eggs has been identified as a factor having notable impact on cod recruitment (Sparholt, 1996; Köster and Möllmann, 1997). Further, also seabirds prey upon early life stages of cod (Myksvoll *et al.*, 2013b). Despite this identification of the species that most likely are the main predators, there are major challenges when attempting to include the effect of predation on mortality of BS cod larvae in models. One reason is that the knowledge of predator distribution in time and space is inadequate. However, there are alternative, indirect, ways of inferring spatio-temporal mortality. Recent work utilizes observed distribution and abundance at two different dates during the pelagic drift phase of BS cod offspring along with a BS cod IBM to quantify combined spatial mortality due to either starvation or predation (Ø. Langangen, Univ. Oslo, pers. comm.).

Larval BS cod face a trade-off between growth and predation mortality. In shallow parts of the water column, there is a higher chance of capturing prey due to increased light, but at the same time a higher risk of being eaten (Fiksen *et al.*, 2007; Vikebø *et al.*, 2007; Kristiansen *et al.*, 2009a). However, turbulence-enhanced feeding rates enable larvae to seek deeper in the water column while maintaining high feeding rates, and thereby reducing mortality caused by visual predators (Kristiansen *et al.*, 2009b).

Demersal 0-group to recruitment to the fishery at age 3

In August, 0-group BS cod are still fully pelagic, but becoming more associated with midwater layers and undertaking diurnal vertical migrations. By October–November, the juveniles have usually become predominantly demersal. The shift from the epipelagic layer to a more demersal habitat confronts the cod with a whole new environment, including different prey and predator species. Table 2 gives an overview of properties and mechanisms suggested to impose interannual variability in survival of BS cod per stage.

Prey

Euphausiids, as already mentioned, dominate the diet of BS cod of age 0 and 1 (Ponomarenko, 1985; Ponomarenko and Yaragina, 2003; Dalpadado and Bogstad, 2004). Survival rates of cod from bottom-settlement to recruitment have been linked to euphausiid abundance (Ponomarenko, 1965, 1979). Still, the newly bottom-settled BS cod adjust to their new surroundings by altering their feeding habits towards becoming more generalists (Ponomarenko, 1958, 1973b, 1984; Dalpadado and Bogstad, 2004). This may be related to their vast distribution range at this stage. Studies conducted at a daily station in the southern Barents Sea, reported by Baranenkova *et al.* (1964), show that the 0-group fish performed daily vertical migrations with highest catches near the surface during night and dawn/dusk hours and in deeper water layers and near the bottom during daylight hours. These vertical migrations were strongly connected with corresponding vertical migrations of euphausiids. The 0-group cod preyed on euphausiids mainly during the night when they ascended to the upper layers, while cod of age 1–3 years fed on them during daylight hours when they descended to near-bottom layers (Baranenkova *et al.*, 1964).

Predation

Young BS cod may serve as a prey for fish (like saithe *Pollachius virens*, long rough dab *Hippoglossoides platessoides*, and skates) and marine mammals (harp seals *Pagophilus groenlandicus* and minke whales *Balaenoptera acutorostrata*; Dolgov *et al.*, 2011; Haug *et al.*, 2011). Still, the most important predators of young cod in the Barents Sea are likely older cod (Yaragina *et al.*, 2009). Dingsør *et al.* (2007) found that predation by subadult cod affects the abundance of cod at age 1, especially in warm years—possibly because of larger overlap between subadult and age-1 cod in warm conditions (Dingsør *et al.*, 2007). Further, the predation mortality on young BS cod seems also to be inversely related to capelin abundance, i.e. cod become more cannibalistic when there is a shortage of their preferred prey species (Hjermann *et al.*, 2004, 2007). Foodweb dynamics thus affects cod recruitment (Hjermann *et al.*, 2007) and this may be an important part of the stock dynamics (Yaragina *et al.*, 2009).

Geographical distribution and ambient temperature

Analyses of spatial data provide new insights into the temporal dynamics of BS cod. Eriksen *et al.* (2011) found some shifts in the distribution of 0-group BS cod during the period 1993–2009, but the central Barents Sea (72–76°N, 15–40°E) was always the main distribution area. Age-1 and -2 cod are generally distributed in the central and eastern part of the Barents Sea (Ottersen *et al.*, 1998; Mehl *et al.*, 2013). Even if the seasonal migrations of age-1 and -2 cod are smaller than for older fish, there is considerable interannual variation in their spatial distribution (Nakken and Raknes, 1987) and their mean ambient temperature may vary considerably between years (Ottersen *et al.*, 1998). This could, at least partly, be due to variability in the extent of eastward displacement during the pelagic stages (Mukhina *et al.*, 1987; Ottersen *et al.*, 2002). It has also been suggested that the spatial distribution of juveniles is density-dependent with abundant year-classes having a more easterly centre of mass (Shevelev *et al.*, 1987; Ottersen *et al.*, 1998). Usually, settled BS cod juveniles can be found over a wider temperature range than larvae and adults and may inhabit less optimal conditions to avoid predation, including cannibalism (Ciannelli *et al.*, 2007). Ciannelli *et al.* (2007) examined the spatial pattern of survival by analysing spatio-temporal data on age-0 and age-1 abundances using generalized additive models. The results suggested that during cold years, juvenile survival increased in the eastern and coldest part of the examined area, which was typically avoided by older conspecifics (Ciannelli *et al.*, 2007).

In some cases, the young BS cod may find themselves in near lethal temperatures. Gerasimov and Tzeeb (1967) considered that the onset of mortality of juvenile cod occurred after prolonged exposure to temperatures from −1.5 to −1.8°C. On the other hand, juveniles have on repeated occasions been caught at temperatures below −1.5°C, then having full stomachs. Given that the temperature tolerance of fish to low temperatures generally depends on their condition (including degree of stomach fullness), one may assume that cod are able to adapt to low temperatures, although abrupt temperature changes are likely to be the most dangerous to them (Gerasimov and Tzeeb, 1967; Tat'yankin, 1974). The presence of antifreeze proteins in cod (Goddard *et al.*, 1999) has recently been shown in BS cod using an original indirect approach (Zhuang *et al.*, 2012).

Statistical analysis of BS cod recruitment

Many authors have analysed historical variations in BS cod recruitment in relation to the fluctuations in various biotic or abiotic factors. A weak point of statistical approaches is that they find patterns, but not the processes behind them. However, such studies are valuable as they may present important quantitative population level information, which is not available through more experimentally oriented work. Further, statistical models, as opposed to numerical models, are driven by the data themselves. The two methods may provide complementary information. In addition, the statistically derived results may provide valuable guidance towards finding the actual mechanistic coupling. The work described in this part of our review does not look at any specific early life stage, but examine links between recruitment (age 3) and explanatory variables directly. Still, these studies point towards particular early life stages and mechanisms described in the preceding stage-by-stage review.

Cyclic fluctuations, regime shifts, and BS cod recruitment

The year-to-year variability in recruitment of BS cod is similar to that in the western Baltic (22–24) and North Sea stocks, but higher than, for example, in the Icelandic cod stock. Compared with other gadoids in the Northeast Atlantic, recruitment of cod is generally less variable than in haddock, but more variable than in saithe (Brunel and Boucher, 2006). The variability in BS cod recruitment has been proposed to be linked to systematic chances in physical properties. One suggestion is based upon that Barents Sea temperature, represented by the mean 0–200 m layer water temperature along the Kola section, undergoes cyclical fluctuations with periods of 4–5, 8–10, and 18–20 years (Izhevskii, 1961, 1964). It has further been argued that the most favourable conditions for establishing a rich year-class of BS cod are when maxima of all three cycles coincide (Izhevskii, 1961, 1964). More recent authors (Elizarov, 1985; Borisov and Elizarov, 1989; Ozhigin *et al.*, 1999) supported the conclusions of Izhevskii based on new material and even suggested that the approach could be used to forecast tendencies in recruitment. However, Ozhigin *et al.* (2003) pointed out that sometimes this approach did not explain year-class strength. Moreover, Ottersen *et al.* (2000) showed that only ~25% of the variability in 1-year temperature forecasts was explained when applying the ordinary least-squares method to eight periodic components (including the three given above). They concluded that the periods suggested by earlier authors are at best quasi-periodic, with their importance varying with time. Titov (2003) suggested that recruitment of BS cod was related to the stratification and chemical composition of Atlantic water masses flowing into the Barents Sea. His hypothesis was connected with cyclic changes of the trophic status of the Barents Sea that oscillated from an internal pattern in periods of weak advection from the Norwegian Sea to an external one in periods of the advection strengthening. It was suggested that strong year classes of fish might appear when the "regime" shifted to the external one. Somewhat related, Sætersdal and Loeng (1987) proposed that appearance of strong or intermediate year classes of BS cod coincided with shifts from "cold" periods to "moderate" or "warm", such shifts being triggered by inflow of Atlantic water. Their plausible ecological explanation lies in the increase in area available for feeding of young cod in warm periods.

Statistical modelling of BS cod recruitment

Recruitment can in principle be predicted from year-class strength at earlier life stages, but, at least for BS cod, the different attempts provide diverging results. Helle *et al.* (2000) showed that an index of early juvenile abundance was a better predictor of recruitment than estimates of SSB, TEP, or age-0 abundance. On the other hand, Mukhina *et al.* (2003) found that a survey-based egg index provided better predictions of age-3 recruitment for BS cod than SSB or abundance indices of later life stages. Although we are not expecting a simple answer, this suggests that an updated analysis of mortalities and abundances at different life stages of BS cod should be performed.

Including other sources of information may enhance the ability of a model to explain recruitment variability. Using a neural network approach, Huse and Ottersen (2003) found that BS cod recruitment for 1974–1999 was best predicted by a combination of spawning-stock biomass, temperature, and capelin biomass. Planque and Buffaz (2008) used quantile regression to investigate if temperature had larger effects on the upper quantiles for BS cod recruitment than the lower quantiles, which was expected if temperature was (or proxy for) a limiting factor. However, the results failed to support significant effect of temperature for the 1943–2002 year classes studied. Svendsen *et al.* (2007) used a coupled physical–biological model to hindcast the oceanographic conditions and primary production in the Barents Sea for 1981–2005 and relate the results to recruitment of BS cod. The results showed a negative relationship with the strength of inflow into the Barents Sea from the southwest in the fourth quarter of the spawning year and a positive relationship with the primary production in the Barents Sea in April the same year. While these two variables explained 70% of the recruitment variability for 1984–2001, the possible causal relation behind the unexpected negative inflow effect found by Svendsen *et al.* (2007) remains unresolved. Other authors have found the temperature–BS cod recruitment link to vary with time. Hjermann *et al.* (2007), studying foodweb effects for the period 1921–1999, found that before around 1950, the temperature–recruitment association broke down. Ottersen *et al.* (2006) reported no significant correlation between temperature and BS cod recruitment around the 1950s and 1960s, but that this changed to a significantly positive relationship in the 1980s and 1990s. Bogstad *et al.* (2013) found a significant positive relationship between sea temperature and residuals from a stock–recruitment model for the 1913–2007 cohorts, but this relationship weakened towards the end of their study period.

Also atmospheric conditions may influence BS cod recruitment. Ottersen and Sundby (1995) found that high recruitment was associated with alongshore southerly windstress anomalies during the period of pelagic drift (from April through summer) and offshore windstress anomalies during egg and larval stages (in April). The NAO (or the Arctic Oscillation—AO) has, during winter season, been the most prominent pattern of atmospheric variability over the middle and high latitudes of the Atlantic sector (Hurrell *et al.*, 2003), but see Overland and Wang (2005, 2010). Its fluctuations have been linked to many ecological patterns (Ottersen *et al.*, 2001). The evidence for NAO effects on BS cod recruitment is, however, mixed. Brander and Mohn (2004) found no significant effect of the NAO on the recruitment of BS cod for the 1946–1998 period, when adding NAO effects to a Ricker-type stock–recruitment model. While the temperature in the Barents Sea was found to be statistically significantly correlated with both the NAO index and with cod recruitment, no significant association was found between the NAO and BS cod recruitment by Dippner and Ottersen (2001), a result similar to that of Sirabella *et al.* (2001). On the other hand, Ottersen *et al.* (2001) did find significant effects of the NAO index on BS cod recruitment for 1972–1997, both when entered alone and in combination with temperature. However, Solow (2002) noted that while strong positive correlations were found between the NAO index and stock–recruitment residuals for BS cod for the years 1973–1995, the correlations changed sign for the years 1946–1972, suggesting that the relationship may be more complex than often thought. This finding was supported by the North Atlantic scale study of Stige *et al.* (2006): the associations between the NAO and cod recruitment changed in magnitude and sign at multi-decadal scales.

Due to sensible management and favourable climate conditions, the BS cod stock has increased considerably in recent years (ICES, 2013; Kjesbu *et al.*, 2014). At present, the total-stock biomass is high, the spawning-stock biomass is record high, the fishing mortality is low, and the age diversity will in a couple of years be comparable

Table 3. Hjort's insights and how they stand the test of time.

Topic	Ideas/important points	Evaluation based upon the knowledge of today	Foundation for evaluation
Recruitment	Importance of recruitment for fluctuations in fish stock abundance	Correct	Hjort (and colleagues on the ICES Migration Committee) demonstrated that fluctuations in stock abundance were strongly influenced by interannual variability in recruitment success. Before Hjort, many attributed the observed variability to varying migration patterns and availability to the fishery (Sinclair, 1997; Houde, 2008).
Critical period	"The numerical value of a year class is apparently determined at a very early stage, and continues in approximately the same relation to that of other year classes throughout the life of the individuals" (Hjort, 1914)	Only partly true—Hjort's view was too narrow	Although the mortality for many stocks is highest during the first months of life, the year-class strength can also be affected considerably at later stages. ". . . recruitment variability was the outcome of complex trophodynamic and physical processes acting over many temporal and spatial scales and throughout pre-recruit life" (Houde, 2008)
Loss of larvae by dispersal ("aberrant drift"; Houde, 2008)	Drift of the larvae into unfavourable places (above the deep waters of the Norwegian Sea, "the great main depression in this region"), might cause mortality of fish	Important, but one of several causes	This idea is further developed in the "member-vagrant" hypothesis, focusing on the role of retentive hydrographic structures, which result in limited dispersal of early life history stages (Sinclair, 1988; Sinclair and Iles, 1989; Werner and Quinlan, 2002)
Depth distribution of juveniles	Young cod stages are found at depths up to 100–200 fathoms (the whole Barents Sea) which is different from more southerly regions, where the younger stages live in shallow water	Correct	Verified by many research surveys
Spawning area	Cod spawning is restricted to banks near the coast	Correct	Verified by many research surveys
Egg quantity poor predictor of year-class strength	Strong year class of cod appeared in 1904 when the quantity of roe taken was small	Partly correct	At Hjort's time, SSB was generally so high that the number of eggs spawned was not a limiting factor for recruitment. When SSB decreases below some threshold, this may be different
Stocks are synchronized in the production of strong year-classes	Strong year classes of all spring-spawning species (cod, haddock, herring) were observed in 1904	Partly correct	Strong year classes of all three species have been observed also more recently, but there are also years where only one or two of the stocks had a strong year class. Ottersen and Loeng (2000) argue for covariability. Bogstad *et al.* (2013) show that the degree of co-variation between the stocks varies with temperature (and thus time)

to that observed in the 1940s. It will be very interesting to see how the recruitment dynamics will evolve in such a situation.

Conclusions—or Hjort's insights and our hindsights

The ideas of Hjort (1914) were indeed pioneering at the time and some remain valid even today, both in general and for BS cod in particular. Still, as we have shown (summarized in Table 2 and Figure 2), early life dynamics of marine fish populations are more complex than Hjort could envisage. Few of his ideas can be considered outright wrong, but several have been modified, supplemented, or expanded by 100 years of international research. The understanding brought forward by Hjort (1914) that recruitment variability is a prominent factor in determining fluctuations in stock size and fisheries remains unchallenged. The "Critical Period" hypothesis is the most well known, but not the only important insight of Hjort (1914). We have summarized and evaluated some of them in a general context, but with BS cod especially in mind (Table 3). The "Critical Period" hypothesis represents, at best, one part of a bigger picture. After many research surveys, data analyses and model runs since Hjort, the accumulated evidence on which life stage recruitment strength is determined is generally inconclusive. Interannual variability is high at all stages and in some years a cohort estimated to be rich at an early stage might have a far weaker abundance estimate at a later stage (pointing towards density-dependence). We can draw the conclusion that mortality at stages other than first-feeding larva is also important for the formation of year-class strength. Moreover, the quest for solving "the Recruitment Problem" has been called off. The current understanding is that variability in recruitment can result from many sources acting throughout prerecruit life (Houde, 2008; Table 2). This overview includes many factors not or only to minor degree considered by Hjort, including turbulence, buoyancy, light, and not least predation. To the latter, we are like Houde (2008) convinced that Hjort must have been aware that predation on cod early-life stages may be important. Still, Hjort ignores the topic to the extent that neither of the words "predation", "predator", or their equivalents are used anywhere in the 234 pages of Hjort (1914).

Acknowledgements

The work was partly funded by the Rearch Council of Norway through the projects *Spatiotemporal variability in mortality and growth of fish larvae in the Lofoten-Barents Sea ecosystem*—SVIM (RCN grant no. 196685/S40) and *Adaptive management of living marine resources by integrating different data sources and key ecological processes*—ADMAR (RCN grant no. 200497/130). The authors wish to thank Dr C. Tara Marshall, School of Biological Sciences, University of Aberdeen, Dr Jon Egil Skjæraasen, IMR, the editor—Dr David Secor, and two anonymous referees, for valuable comments to an earlier version of the manuscript. Karen Gjertsen, Hildegunn Mjanger, and Erik Berg, all IMR, are thanked for help with Figure 3.

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Handling editor: David Secor

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2088–2100. doi:10.1093/icesjms/fst202

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Intermittent recruitment and exploitation pulse underlying temporal variability in a demersal deep-water fish population

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Bergstad, O. A., Øverbø Hansen, H., and Jørgensen, T. Intermittent recruitment and exploitation pulse underlying temporal variability in a demersal deep-water fish population. – ICES Journal of Marine Science, 71: 2088–2100.

Received 27 June 2013; revised 26 October 2013; accepted 28 October 2013; advance access publication 29 December 2013.

Recent temporal variability in abundance, size and age structure, distribution, and recruitment of the Skagerrak population of the commercially exploited long-lived deep-water demersal macrourid roundnose grenadier (*Coryphaenoides rupestris*) appeared strongly influenced by a combined effect of a single pronounced recruitment incident in the early 1990s and a subsequent pulse in targeted exploitation a decade later. Fishery-independent annual survey data showed that probably only one strong year class occurred across an almost three-decade period, 1985–present. Recruitment studies in deep-water fish remain few, yet rarity of successful recruitment events may have to be added to life-history characteristics already recognized as limiting the potential for sustainable harvesting of deep-water demersal fish, i.e. extended lifespan, slow growth, high age at first maturity, and low fecundity.

Keywords: grenadier, Macrouridae, population dynamics, Skagerrak.

Introduction

Overexploitation of deep-water fish species often result from too high exploitation rates being applied to populations with low productivity rates and thus low resilience to enhanced mortality rates caused by fishing (e.g. Large *et al.*, 2003; Gordon, 2005; Clark *et al.*, 2007). Low productivity rates reflect life-history strategies in many deep-water species that are characterized by long lifespan, relatively low fecundity, slow growth, and high age at first maturity, which are regarded as adaptations to the generally reduced production rates in deep-water ecosystems (e.g. Merrett and Haedrich, 1997; Drazen and Haedrich, 2012).

Since Hjort (1914), it has been duly recognized that the variation in the recruitment rate in most fish populations dominates temporal abundance patterns as well as age and size distributions. Hence, recruitment has been studied extensively and monitored closely. Most of this effort has been restricted to epipelagic and demersal neritic fish species and populations. In studies of deep-water species, however, recruitment variation has received comparatively little attention despite being recognized as potentially significant for, for example, orange roughy (*Hoplostethus atlanticus*; e.g. Clark, 2001), for which recruitment appears to be highly episodic and very low for extended periods of time (e.g. Koslow *et al.*, 2000). Studies of a macrourid *Macrourus berglax* by González-Costas (2010) and *Sebastes mentella* by Planque *et al.* (2012) also suggest substantial variation and extended periods of low recruitment. High recruitment variation may seem intuitively incompatible with the generally conservative life-history strategies observed in many deep-water species. However, that is an assumption rather than an observed trait, and recruitment variability would seem to deserve further study also in deep-water populations. The general level of variation may be higher than often assumed, but it is also possible that the incidence of good year classes may be low. If the latter is the case, then resilience to exploitation may be different than in populations with steady less-variable recruitment rates.

In this study, we were interested in exploring to what extent deep-water fish population traits such as size structure, abundance, and distribution vary as a combined effect of variable recruitment and the commercial landings history. One of the reasons underlying the virtual lack of studies of recruitment variation and its influence on population traits is that few sufficiently long time-series of relevant data exist. In this study, we utilized a fishery-independent data-series providing information for almost three decades on what appears to be a self-contained commercially exploited population of a demersal deep-water fish.

The roundnose grenadier (*Coryphaenoides rupestris*) is a commercially harvested North Atlantic long-lived fish (Lorance *et al.*, 2008) of the prominent deep-water family Macrouridae (Iwamoto, 2008). In our study area, the Skagerrak (ICES Divisions IVa and IIIa), the grenadier reaches ages of ≥70 years and attains maturity at the age of 8–12 years (Bergstad, 1990). Studies of the biology and ecology of roundnose grenadier in the Skagerrak have been rather extensive (Bergstad, 1990; Bergstad and Gordon, 1994; Mauchline *et al.*, 1994). Based on the apparently restricted distribution patterns of juveniles and adults, and the observation of spawning and occurrence of mesopelagic eggs and larvae, it has been suggested that the grenadier in Division IIIa and the eastern part of Division IVa constitutes a population separate from those in other waters (ICES, 2012a). Spawning occurs in late autumn, and following an extended mesopelagic egg and juvenile period, the grenadier attains a demersal lifestyle in late summer–early autumn in the following year (Bergstad and Gordon, 1994). It is unlikely that there is significant migratory exchange across the comparatively shallow sills to neighbouring fjords or western Norway continental shelf deeps. Recent molecular genetics analyses provide further support for the existence of an isolated population in the Skagerrak (Knutsen *et al.*, 2012). Abundance estimates for the Skagerrak in 1987 based on swept-area statistics from trawl surveys ranged from 33 000 to 75 000 t (Bergstad, 1990).

For many years, the grenadier was only taken as bycatch in bottom trawl fisheries for *Pandalus borealis* and perhaps *Nephrops*. The interest in marketing bycatches and developing targeted fisheries grew in the 1980s, probably stimulated by the then new fisheries west of the British Isles and enhanced marketing opportunities. In the subsequent decades, a few vessels landed small quantities for local markets and export, and one or two Danish vessels specialized in grenadier fishing, producing landings for human consumption and reduction. Reported landings thus constituted the sum of the landed fraction of the bycatch and the catches resulting from directed grenadier fisheries. The discarded bycatch is unknown, but since grenadier could be landed in Denmark for reduction, it is likely that a rather large fraction was landed. This may not have happened in Norway or Sweden, where there has been almost no or only sporadic marketing opportunities for this species. Estimates of the Norwegian bycatch varied between a few hundred and 2500 t, but have declined in recent years (ICES, 2012a), possibly as a result of sorting grids that were introduced on a voluntary basis in the mid-1990s in the *P. borealis* fishery. A major expansion of the directed fishery for grenadier in 2003–2005 resulted in landings at unprecedented levels (Figure 1), and this event was followed by a moratorium effective from mid-2006 onwards.

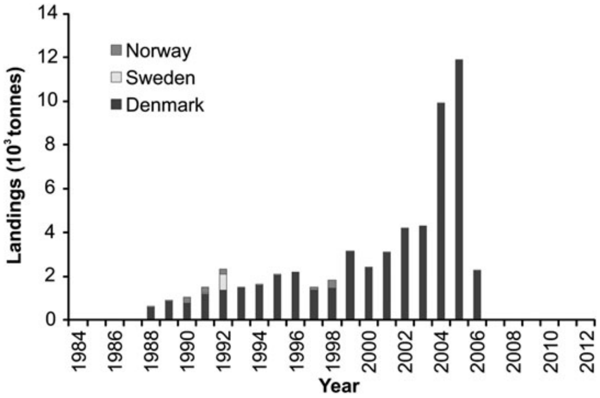


Figure 1. Landings of roundnose grenadier from ICES Divisions IIIa and IVa during the period of study, 1984–2013 (ICES, 2012a). The targeted fishery ceased in 2007.

The life-history strategy of the grenadier and the limited area of distribution below 300 m in the deep Skagerrak (where the maximum depth is 720 m) made the population in this area a good candidate for studies of population-level natural and fishery-induced variability.

Data utilized in this account were collected on annual research vessel surveys through the period 1984–2013, and we analysed temporal variation in abundance and biomass, size and age distribution, occurrence of juveniles, and spatial distribution. The null hypothesis of the study is that these population traits varied without trends or patterns through the time-series. We also specifically examined variation in relation to the exploitation history.

Material and methods

For the biological analyses, we used data from an annual fishery-independent research survey conducted by the Institute of Marine Research, Norway. The primary objective of this investigation is to monitor deep-water shrimp (*P. borealis*) in the deeper parts of the northeastern North Sea and the Skagerrak, but comprehensive data on the fish community is also maintained. Hence, catches of roundnose grenadier, in terms of numbers and weight, were recorded during the entire 1984–2013 survey series. The survey is run as a depth-stratified survey with the aim to sample the same total area and set of fixed locations every year, i.e. within the deeper parts of ICES Divisions IVa and IIIa. The vessels used were RV "Michael Sars" and RV "Håkon Mosby", sister ships with identical engines, both rigged as stern trawlers, and operating the same trawls. However, although the overall standardization was maintained throughout the series, some variation and significant changes were unavoidable. In some years, weather conditions reduced the number of tows significantly. Two different, but of similar size, double-warp otter trawls were used. Gear information as well as key changes and events that may have affected the grenadier sampling and data are provided in Table 1. To reduce the variability of trawl geometry with varying depth, a restriction rope between the warps (known as "strapping") was used on a routine basis since 2008. Except in 2004/2005, when conducted in May, the survey has been carried out in autumn or winter (October–November or January–February). In the 1984, 2003, 2006, and 2007 surveys, no tows or only a single tow were made deeper than 400 m; these years were excluded from the analyses.

For each trawl tow, all individuals or a random subsample of roundnose grenadier were measured (pre-anal fin length, PAFL) and allocated to 1.0 cm size classes. Thus, the following dataseries spanning the period 1985–2013 were available for analyses:

(i) geo-referenced standardized catches by number and weight per 1 h trawling from areas 300 m and deeper, i.e. the full depth range of the grenadier in this area (Bergstad, 1990);

(ii) length frequency distributions by catch;

(iii) geo-referenced standardized catches by number of small juveniles of PAFL ≤ 5 cm.

For selected years, i.e. 1987 and 2007–2013, age distributions were derived using age determination by transverse sections of sagittal otoliths as developed by Bergstad (1990) and later used by other workers (Gordon and Swan, 1996; Kelly *et al.*, 1997; Allain and

Table 1. Summary of data on the bottom trawl survey series, 1984–2012.

Year	Survey month	Vessel	Trawl	Groundgear	Vertical opening (m)	Wingspread (m)	No. trawls (300–400) m	No. trawls ≥400 m
1984	October	MS	ST		4	18	9	1
1985	October	MS	ST		4	18	16	5
1986	October/November	MS	ST		4	18	15	9
1987	October/November	MS	ST		4	18	21	14
1988	October/November	MS	ST		4	18	20	11
1989	October	MS	C	R	4.5	13	24	7
1990	October	MS	C	R	4.5	13	21	5
1991	October	MS	C	R	4.5	13	19	9
1992	October	MS	C	R	4.5	13	17	10
1993	October	MS	C	R	4.5	13	20	10
1994	October/November	MS	C	R	4.5	13	17	10
1995	October	MS	C	R	4.5	13	17	12
1996	October	MS	C	R	4.5	13	16	11
1997	October	MS	C	R	4.5	13	19	6
1998	October	MS	C	R	4.5	13	17	6
1999	October	MS	C	R	4.5	13	19	8
2000	October	MS	C	R	4.5	13	15	10
2001	October	MS	C	R	4.5	13	14	4
2002	October	MS	C	R	4.5	13	18	6
2003	October/November	HM	ST		4	18	13	0
2004	May	HM	C	R	4.5	13	11	6
2005	May	HM	C	R	4.5	13	15	8
2006	February	HM	C	R	4.5	13	10	0
2007	February	HM	C	R	4.5	13	10	1
2008	February	HM	C[a]	R	4.5	13	13	5
2009	January/February	HM	C[a]	R	4.5	13	18	7
2010	January	HM	C[a]	R	4.5	13	17	7
2011	January	HM	C[a]	R	4.5	13	15	7
2012	January	HM	C[a]	R	4.5	13	15	5
2013	January	HM	C[a]	R	4.5	13	20	8

MS, RV "Michael Sars"; HM, RV "Håkon Mosby"; ST, shrimp trawl (see text); C, Campelen 1800 (Engås, 1991); R, rock-hopper groundgear. All the trawls were fitted with a 6-mm mesh liner in the codend.

[a] Strapping was facilitated by a 10-m rope connecting the trawl warps 200 m in front of otter doors.

Lorance, 2000). The age readings obtained by this method were validated for young fish by Gordon and Swan (1996).

Furthermore, in April 2007, supplementary data and otoliths were obtained from a deep-sea fish survey in the northeastern North Sea and Skagerrak on the RV "Håkon Mosby". Five tows with the Campelen 1800 bottom trawl were carried out in the central Skagerrak to sample roundnose grenadier and greater argentine (*Argentina silus*).

Results

Abundance and biomass

Estimates of abundance and biomass in the research survey varied substantially within single surveys and through the time-series 1985–2013 (Figure 2). A source of error was the variation in the level of sampling effort in the main depth range of the grenadier, i.e. at depths exceeding 400 m. There was an apparent increase in abundance and, to a lesser extent, biomass from the 1980s through the 1990s until about 2005. Unusually, high abundance was observed in 2004 (the survey in that year was conducted in May rather than in winter). In the most recent years, 2008–2013, the estimates were lower than in the preceding 10–15 years and similar to or lower than in the 1980s.

Size and age composition

Size frequency distributions for each year of the time-series are shown in Figure 3a. There was a major change in the distributions at the beginning of the 1990s when the proportion of specimens with PAFL >15 cm declined markedly. This pattern persisted until the end of the series. In 1991–1992, a mode of small fish appeared that can be tracked through the subsequent years until the mid-2000s.

The size distribution from the deep-sea fish survey in April 2007 (Figure 3b) was unimodal, and the modal length was somewhat lower than in the *Pandalus* survey 2 months earlier (Figure 3a). Both the largest and smallest fish were absent from these distributions, collected in the year after which the directed fishery ceased.

Age data were only available from the deep-water fish survey in April 2007 and the shrimp survey catches from 2008 to 2013 (Figure 4). The age distribution from 1987 extracted from Bergstad (1990) contrasts substantially with the distributions from the recent period 2007–2013 in terms of proportions of old fish (e.g. >20 years) in the samples. In recent years, however, the proportion of old fish has increased, yet remained low compared with the level in 1987.

Abundance of juveniles

The interannual variation in the abundance of grenadier of PAFL ≤5 cm is shown in Figure 5. Periods of 3–4 years with elevated abundance occurred in 1991–1994 and 2002–2005, with intervening periods of very low abundance, but only 1992 had exceptionally high abundance. According to growth estimates from

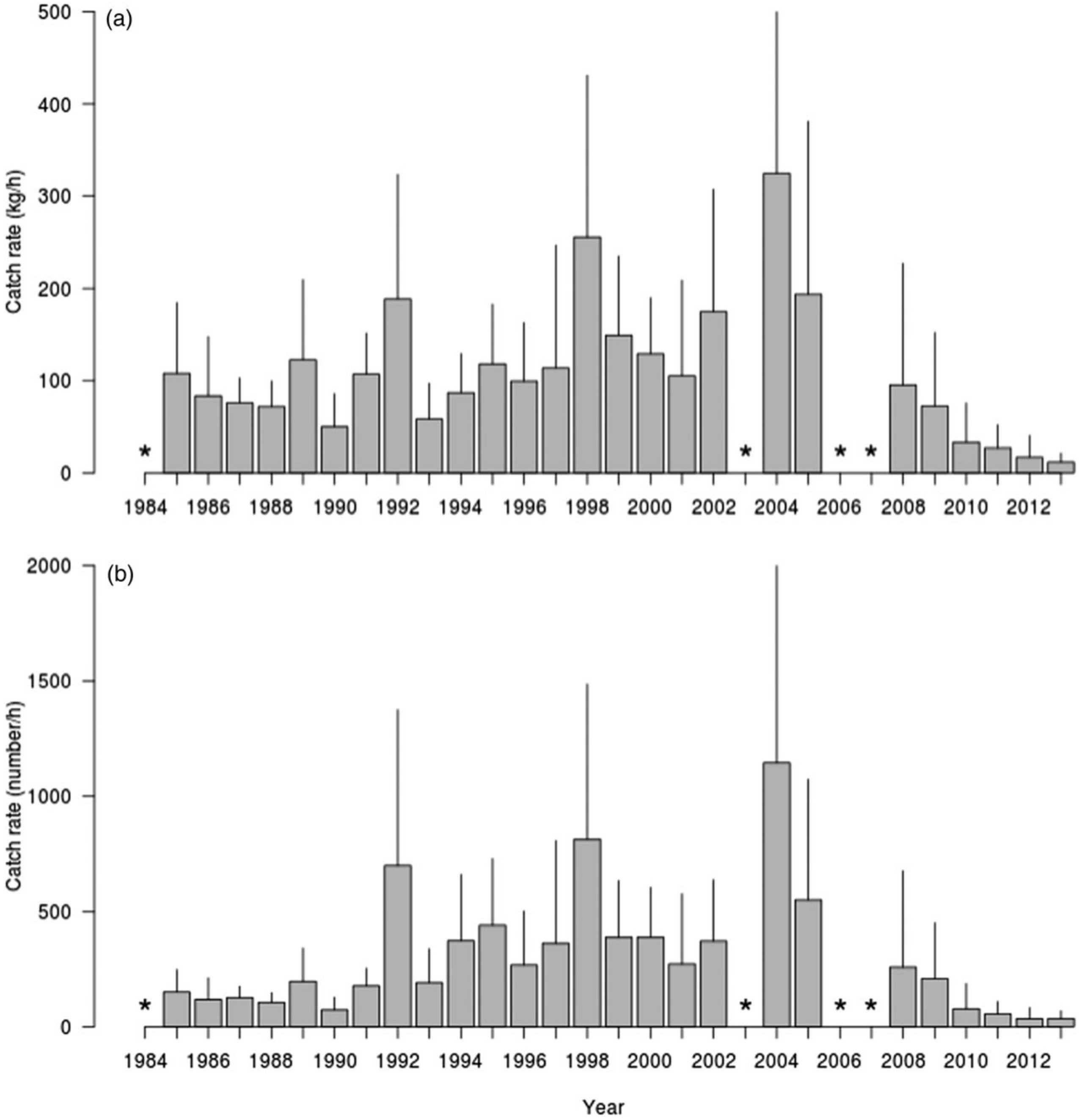


Figure 2. Standardized survey catches of grenadier, 1985–2013 (circles), and associated box and whisker plots. (a) Biomass (kg h^{-1}). (b) Abundance (no. h^{-1}). *In 1984, 2003, 2006, and 2007, only a single or no trawls were made deeper than 400 m, and data from those years were excluded.

Bergstad (1990) and Bergstad and Gordon (1994), the PAFL ≤5 cm size class would mainly comprise age groups 0 and I, perhaps also some from age group II (the size at the end of the 0-group stage is 2.5–3.0 cm).

Geographical distribution

The geographical distribution of positive catches within the 1985–2013 survey series is illustrated in Figure 6. The overall distribution area did not vary substantially, and the distribution pattern is similar from year to year. The declining abundance in recent years occurred across the entire distribution area of the population.

Discussion

The grenadier is a bentho-pelagic species that tends to occur in aggregations (Bergstad, 1990); thus, some of the extensive scatter in abundance and biomass between catches in individual survey years may reflect patchiness in distribution. Furthermore, some of the variability between years reflects the somewhat variable sampling effort and sampling time between years. Abundance in 2004

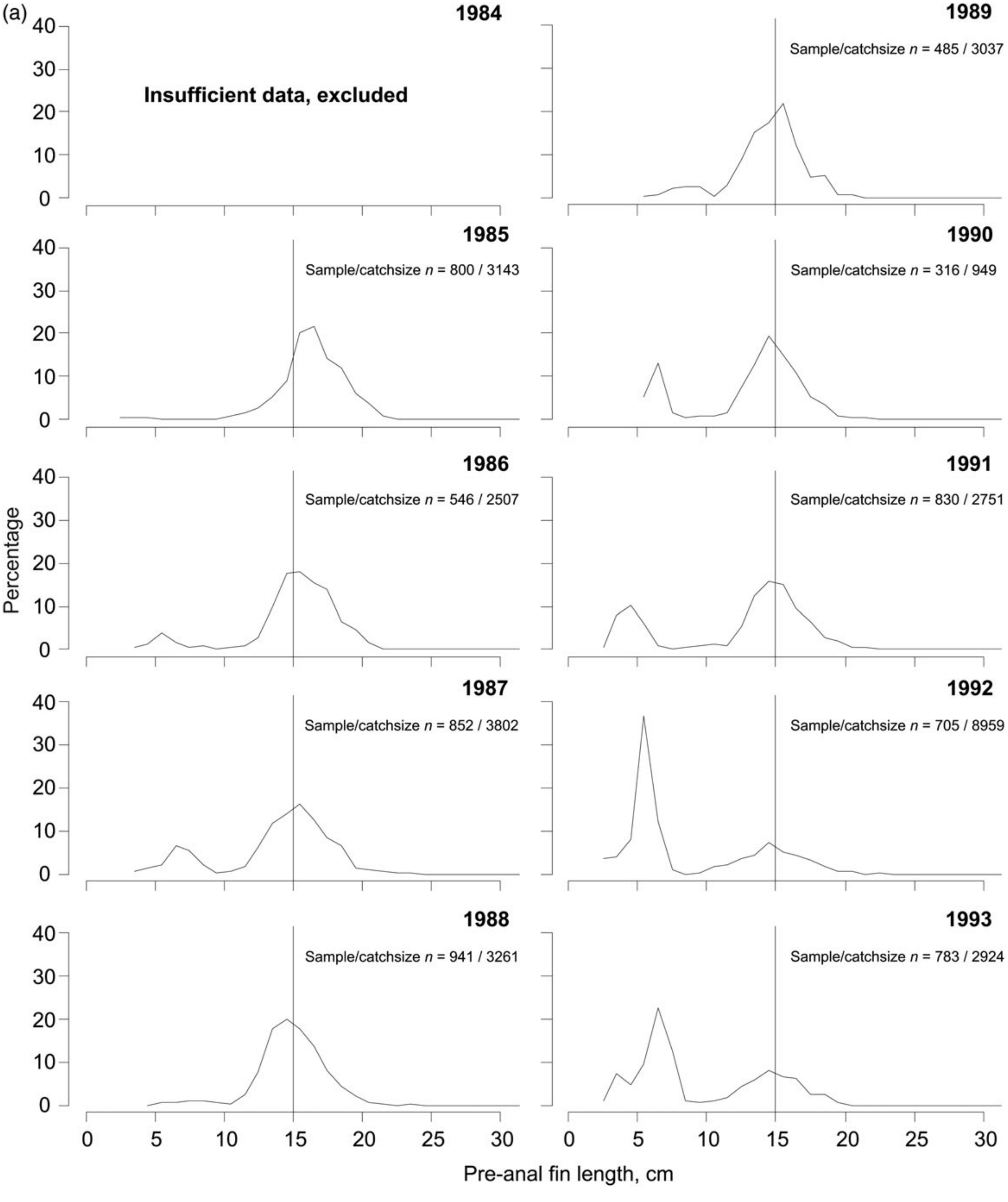


Figure 3. (a) Length distributions of roundnose grenadier from annual *P. borealis* surveys, 1985 – 2013. Length is measured as PAFL (in cm). The distributions are calculated as percentage by numbers of fish in each centimetre length interval standardized to total catch number and trawling distance for each station each year. (b) Length distributions of roundnose grenadier from five bottom trawl catches in the central Skagerrak, April 2007, RV "Håkon Mosby"; $n =$ number of individuals captured and measured.

was exceptionally high, and this was the first of only 2 years when the survey was conducted in May rather than in autumn and winter. Light levels are similar in late autumn and winter, and data from those seasons would likely be comparable, but comparing May–June with the dark seasons may be more uncertain. Seasonal abundance or catchability variation has not been observed for this deep-living species in this area, but a seasonal pattern cannot be excluded as a source of variation.

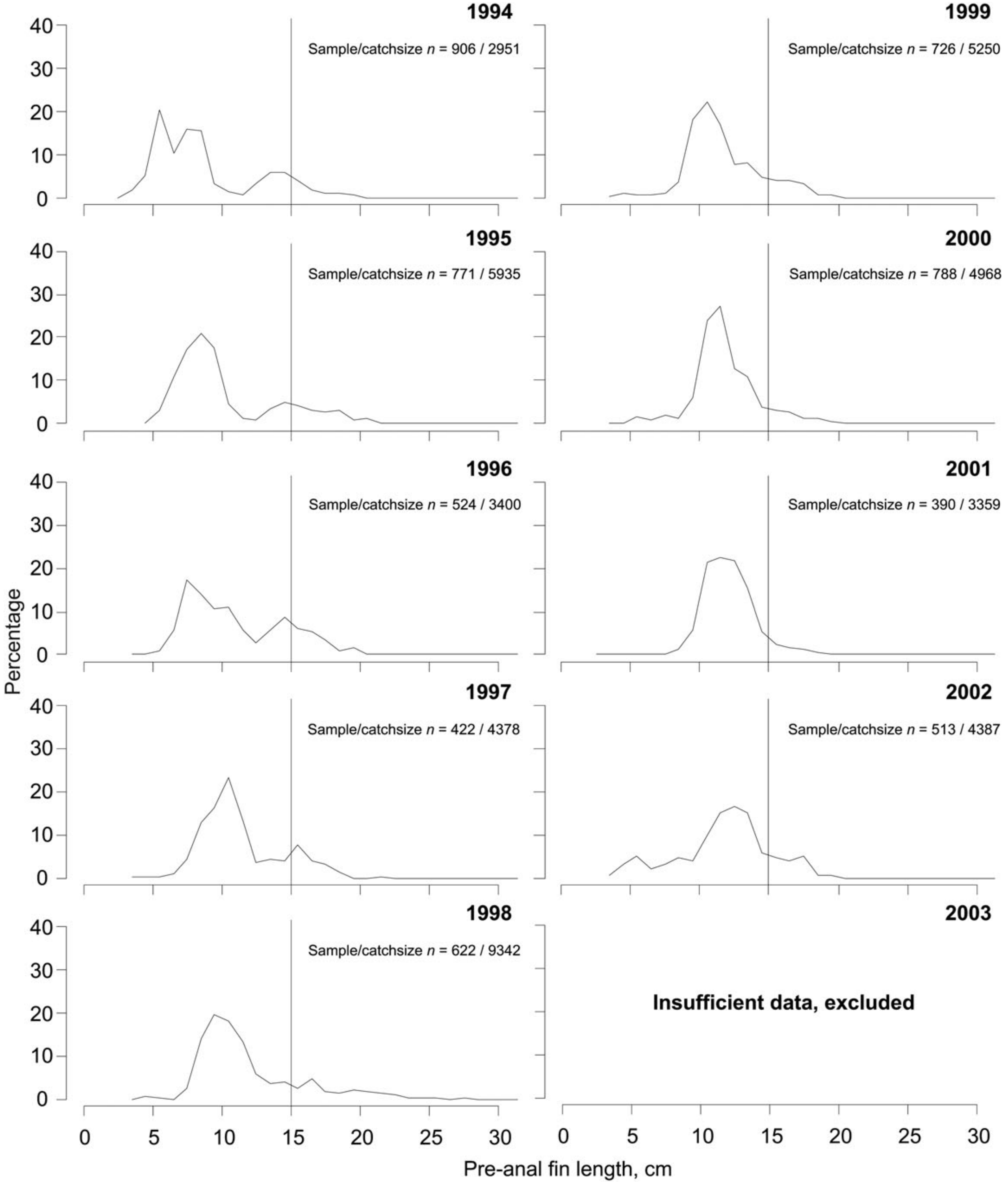
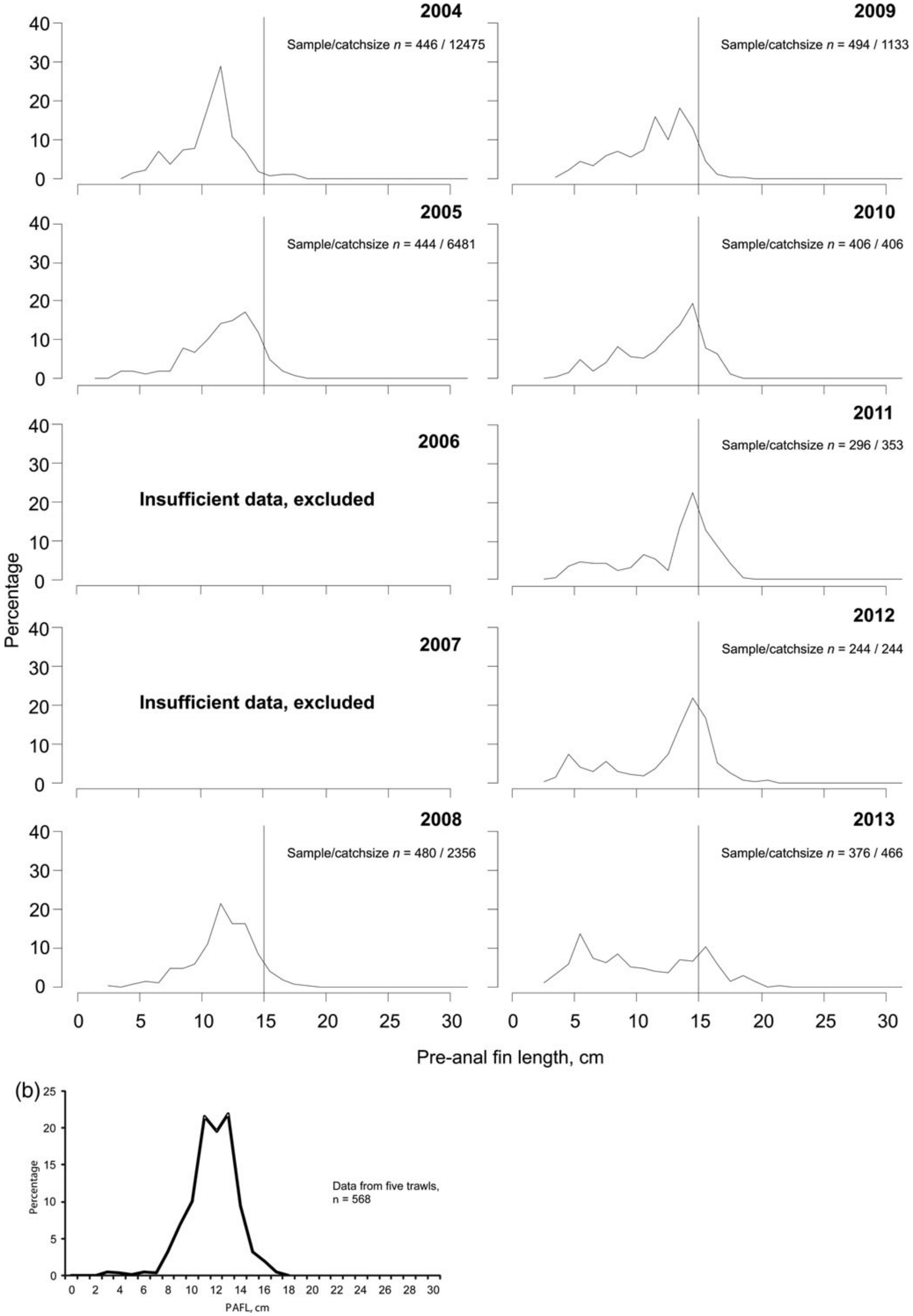


Figure 3. Continued

The time-series suggests, however, rather extensive variation, perhaps more extensive than expected for a long-lived species like roundnose grenadier. Moreover, despite substantial interannual variation, a long-term increasing trend in abundance and biomass was suggested from the late 1980s through the 1990s until 2004/2005. After that, there is some uncertainty due to the unfortunate weak sampling in the two subsequent years. However, the more reliable estimates from 2008–2013 suggest a decline to the level observed in the late 1980s or even lower levels.

Increased abundance in the mid-2000s coincided with an increase in landings. Landings before 1988 were small or at the level observed in the early 1990s. Danish landings were always dominant,



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and Norway and Sweden and all other nations reported very minor landings. Until 2003, landings were increasing, but below 4000 t year^{-1}. In 2004–2005, landings increased sharply to more than 10 000 t year^{-1}. According to Danish information reported in 2005 (ICES, 2005), two vessels targeted greater silver smelt (*A. silus*) and roundnose grenadier in 2004. Another vessel joined the fishery after that. Most of the Danish landings of roundnose grenadier were used for reduction. Following consultations between the EU and Norway, the directed fishery was closed by the end of April 2006 and has remained closed since.

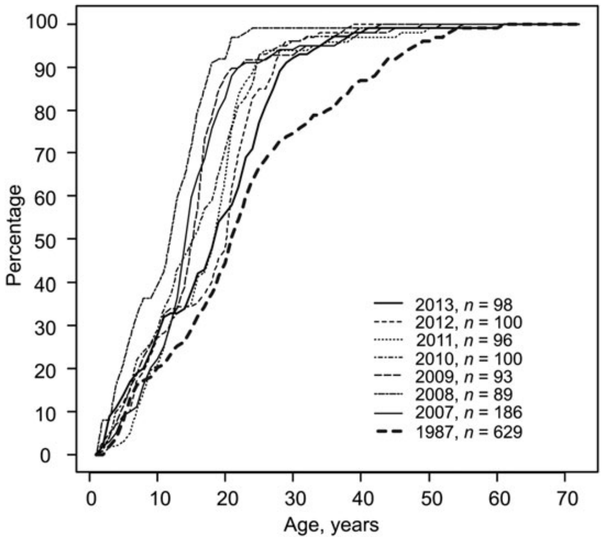


Figure 4. Cumulative age distributions of roundnose grenadier in the Skagerrak. Data from survey catches in the Skagerrak in 1987 and 2007–2013. The distribution from 1987 was modified from Bergstad (1990). Data from 2007 were collected on the deep-water fish survey in April.

The survey results suggest a continued decline in abundance after the strong pulse in landings from the targeted fishery in the mid-2000s. The recent abundance is at levels at or below those observed in the early 1980s preceding targeted fisheries.

The abundance of juveniles of PAFL ≤5 cm was highly variable across the time-series. Pulses of elevated abundance appear to be followed by many years with very low abundance, and the strong recruitment event in the early 1990s was particularly prominent. There are no age data from that period so it is not possible to determine if this event was produced by a single or several year classes. The progression of the mode in the size distributions from 1991 on, however, suggests that only a single year class "rejuvenated" the population in that period. In April 1992, a cruise with a limited bottom trawl sampling of deep-water fish was conducted (Bergstad, unpubl. data), and the mode of very small fish of PAFL around 5 cm was prominent already at that time. It is likely that that mode represented the recently settled juveniles resulting from spawning in late 1990 or early 1991.

What appears as an elevated production of juveniles in the early 1990s probably explains the higher abundance of the population ~10 years later, i.e. in 2003–2005.

In 2008–2013, the size distributions were dominated by much smaller fish than in the 1980s when abundance was similar. Fish of PAFL >15 cm that were prominent in the 1980s were almost absent in recent years. It is conceivable that what appears as a strong pulse in exploitation in 2003–2006 depleted the strong year class(es) from 1991 and adjacent years and resulted in the substantial change in size structure and the reduced abundance in subsequent years.

The age distribution from 1987 (modified from Bergstad, 1990) represents a period before both the recruitment event in the early 1990s and the enhanced exploitation in the mid-2000s. Unfortunately, no age data were collected in the period 1989–2006, during which both the recruitment event and harvesting

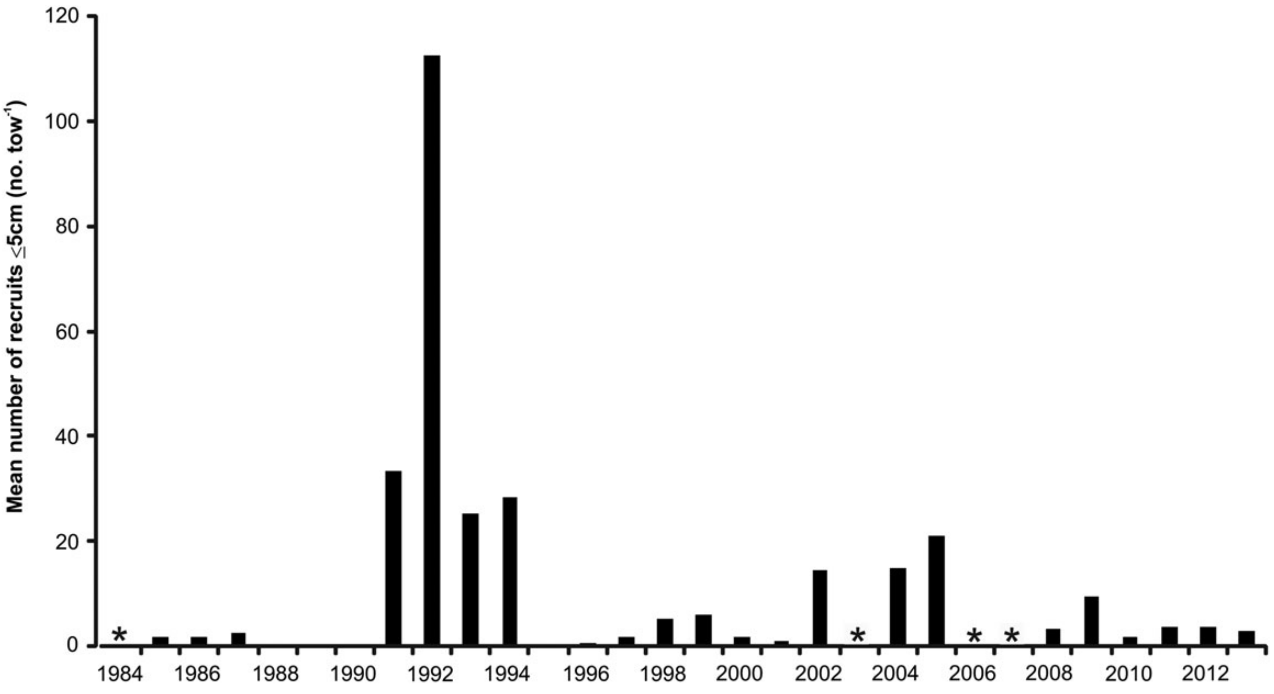


Figure 5. Mean catch of roundnose grenadier of PAFL ≤5 cm, 2005–2009. Data from shrimp survey, trawls deeper than 300 m. *In 1984, 2003, 2006, and 2007, no trawls were made deeper than 400 m, and data from these years were excluded.

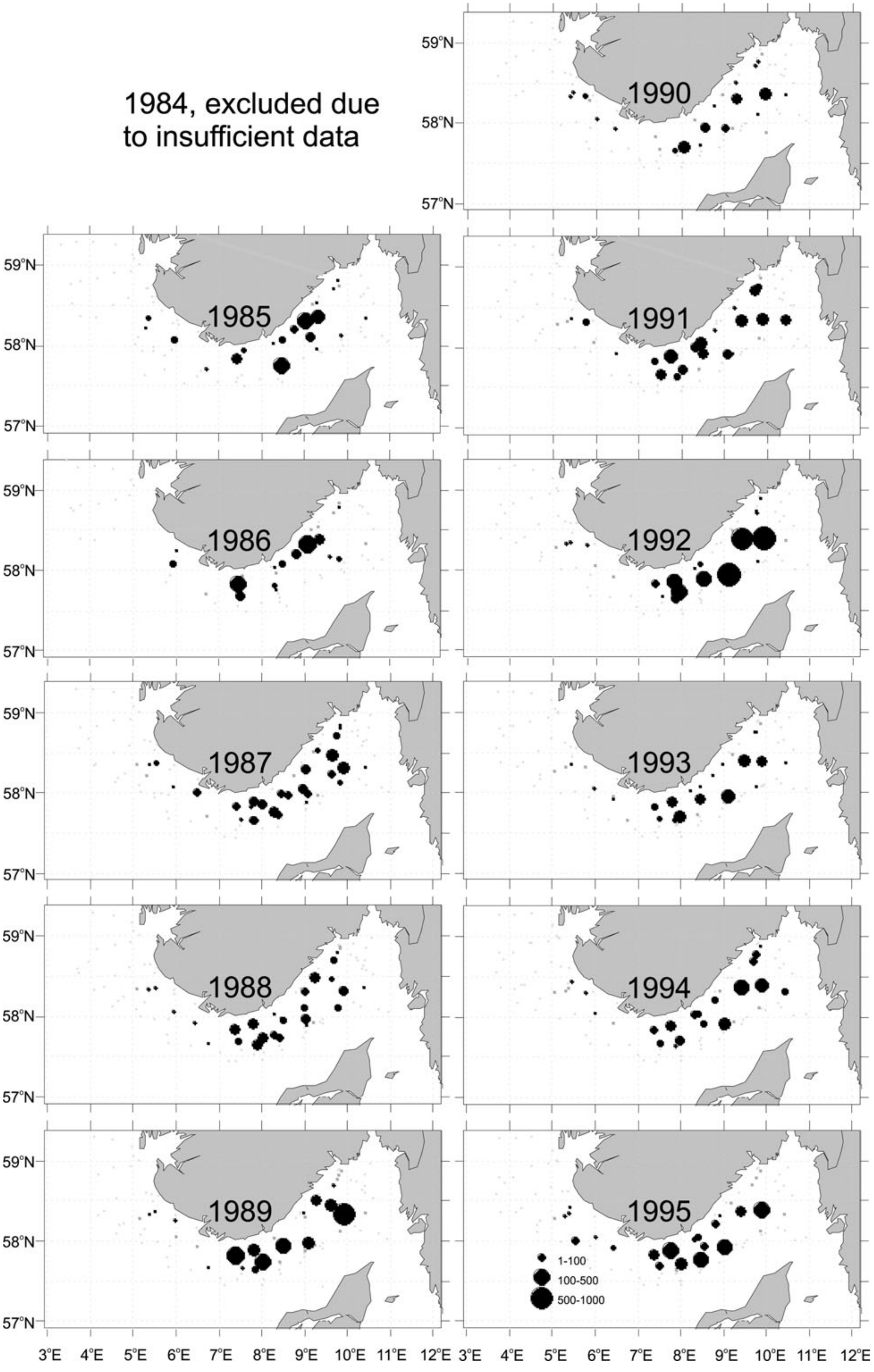
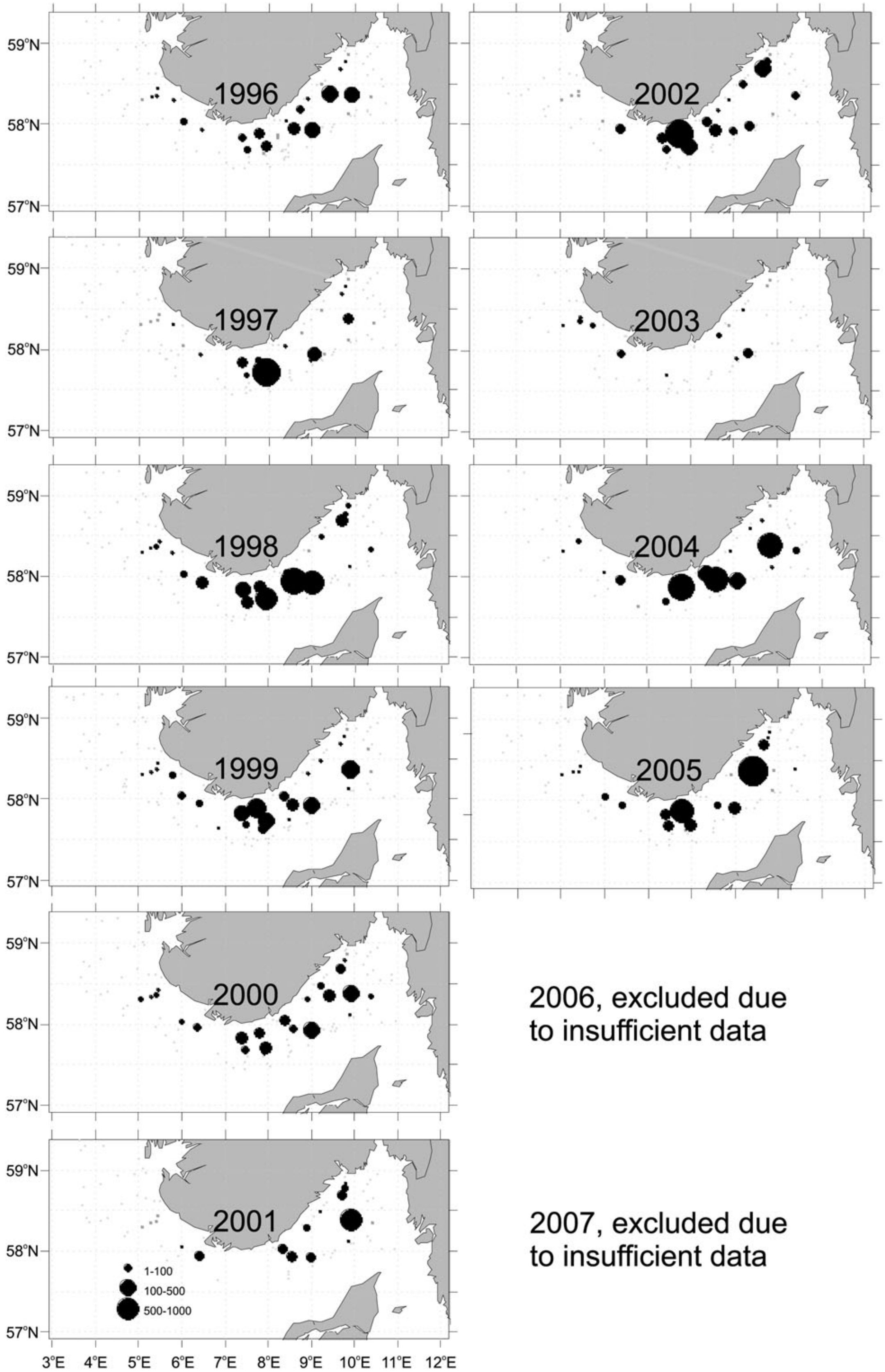


Figure 6. Geographical distribution of catches of roundnose grenadier (kg h^{-1}). Data from shrimp survey, trawls deeper than 300 m. Grey circles are trawls with no catch of grenadier.



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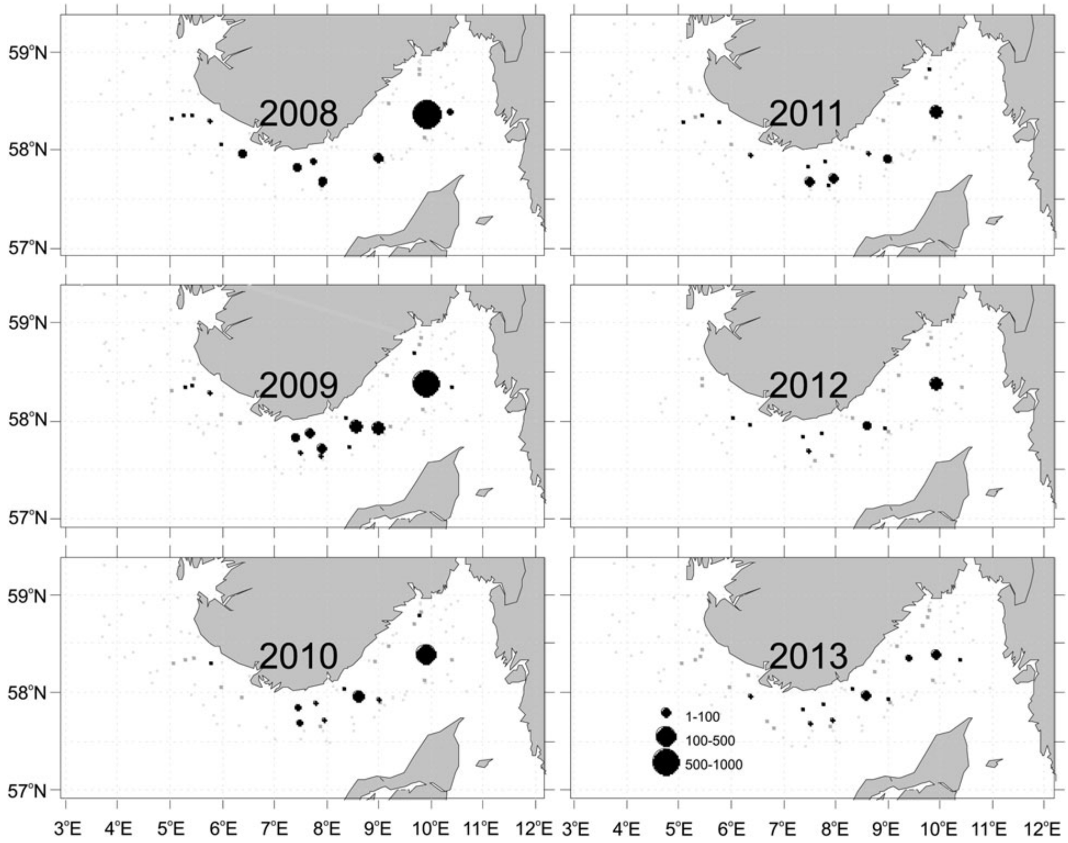

Figure 6. Continued

had the strongest structuring influence on the population. In the period 2007–2013, i.e. past the exploitation pulse, age distributions with much reduced proportions of old fish reflect the combined result of the generally low recruitment after the early 1990s and the exploitation before the moratorium introduced in 2006. The increasing proportion of old fish throughout the period 2008–2013 presumably reflects ageing of the population in a situation of reduced rejuvenation rates. Generally, enhanced recruitment or another recruitment event as in the 1990s will probably be needed to facilitate growth in the ageing population.

The geographical distribution within ICES Divisions IIIa and IVa was described earlier based mainly on data from a single year (Bergstad, 1990), but the temporal variation within this area has not been studied previously. The geo-referenced survey catches do not suggest substantial temporal variation in spatial distribution.

The more striking result of this study is the occurrence of what appears to be a single substantial recruitment event across a time-series of almost three decades, and it is likely that this represented a single year class born in 1991. The abundance of juveniles in that year was tenfold or more above the average for all other years. This recruitment pulse caused lasting demographic changes in the population and probably resulted in the enhanced abundance and biomass in the early 2000s.

The few previous studies of deep-sea demersal fish species recruitment also demonstrated considerable variation, although not across such a long time-series. Survey data on beaked redfish (*S. mentella*) in the Barents Sea suggest periods of several years of elevated recruitment followed by a near decade-long recruitment failure (Planque *et al.*, 2012). For deeper-living species such as the macrourid roughhead grenadier (*M. berglax*) in the Northwest Atlantic, Spanish and EU scientific survey series from 1994 to 2009 showed strong recruitment variation and a single very prominent 2001 year class (González-Costas, 2010). These studies and the Skagerrak grenadier data also suggest that, for deep-water species with extended lifespans, substantial recruitment variation and rare strong year classes or pulses in recruitment should be expected. Recruitment variation should also be expected to affect population structure and abundance.

The Skagerrak observations furthermore suggest that the unregulated fishery may have responded to a real increase in abundance and biomass in the early 2000s. Most of the catch was landed for reduction, so even if the grenadier were predominantly comparatively small, they were still marketable in unlimited quantities. There are indications that fishing effort increased in the years before the introduction of regulations in 2006 (i.e. new vessels entered the fishery). Survey abundance subsequently dropped to the low levels of the 1980s. In itself, that would not cause major concerns, but the size and age structure also changed considerably and indicated wider population-level effects. It is thus probable that the fishery had the combined effect of eroding both the accumulated fraction of very old fish of around 30 years of age and older that dominated the population in the mid-1980s (Bergstad, 1990) and the medium-age fish resulting mainly from the single recruitment pulse in the early 1990s. The current low abundance and truncated age structure in the population thus reflects both the exploitation and recruitment history spanning the past 2–3 decades.

The experience is not new that an unregulated fishery faced with elevated abundance and opportunities expands beyond sustainable catch levels and affects population size and demography (e.g. Cushing, 1968; Dragesund *et al.*, 1980), also in deep-water species (e.g. Clark, 2001; Large *et al.*, 2003; Gordon, 2005; Clark *et al.*, 2007; Lorance *et al.*, 2008). The Skagerrak grenadier population was not monitored very closely in the early 2000s by any party, and the expansion in landings happened very quickly. In essence, the fishery was "booming" for 1–2 seasons before anyone reacted with some concern that the landings were probably increasing beyond any perceived sustainable level. ICES did not sound any alarm bells, and management reacted to expressions of concern from other parties.

In retrospect, the lesson learned is that it cannot be taken for granted that recruitment variation is any less influential on population dynamics in deep-sea species than in epipelagic and neritic species. Thus, monitoring and management strategies of deep-sea fish and fisheries must take recruitment variation into account. If good year classes can only be expected rarely, as in the Skagerrak grenadier, then variation in recruitment should be added as yet another life-history strategy trait that can enhance the vulnerability of deep-sea fish populations.

Questions for further studies relate to mechanisms underlying recruitment variation in this and other long-lived deep-sea species, specifically the cause of the apparent enhanced survival of grenadier juveniles in 1991–1992. A thorough analysis of this issue was beyond the scope of this paper. The only significant fishery in this area that might have influenced the survival rate of juvenile grenadier is the *P. borealis* fishery, but there are no indications of any temporal variation or trends in this fishery, e.g. depth range, mesh sizes, effort level, that would suggest that the pattern of grenadier recruitment reflects variation in commercial bycatch. In the Norwegian shrimp fishery, fishing effort varied without trend until the early 2000s, then declined (Munch-Petersen *et al.*, 2011). Preliminary examination of time-series of deep-water temperature and salinity, and recruitment data for *P. borealis* in the Skagerrak suggested no obvious relationship, and no particular feature correlated with the grenadier recruitment event in the early 1990s. The grenadier spawns in late autumn in the Skagerrak, and the eggs and larvae are primarily found in deepwater, i.e. deeper than 150 m, and the pelagic juvenile phase lasts for 6 months or more during which calanoid copepods and other planktonic crustaceans are the main prey (Bergstad and Gordon, 1994). The juveniles are mesopelagic and apparently depend on vertically migrating or deep-living overwintering copepods. Recently settled benthopelagic juveniles of the grenadier also feed on pelagic crustaceans, primarily mysids (Mauchline *et al.*, 1994). It may be hypothesized that the abundance of calanoid copepods and thus feeding and survival conditions for grenadier juveniles in the deep water vary due to (i) local abundance and vertical migration patterns of copepods and (ii) advective production resulting from the Atlantic inflow from the Norwegian Sea. Unfortunately, neither do relevant local zooplankton production data for the Skagerrak exist for the entire time-series nor direct measurements of advective production. Advective production would probably be well correlated with inflow rates and as one of the major physical features of the North Sea and Skagerrak, the Atlantic Inflow is well studied for the period 1985 on (ICES, 2012b). It appears that the early 1990s recruitment event happened when the inflow was at a maximum. This observation may form a starting point for further testing of emerging hypotheses on processes underlying the varying and apparently intermittent recruitment of the Skagerrak grenadier and other deep-sea species.

Acknowledgements

We are grateful to the many IMR colleagues led by the PIs Stein Tveite and Guldborg Søvik who sampled grenadier on the *Pandalus* surveys 1984–2013. We are also grateful to two anonymous reviewers whose constructive comments improved the manuscript.

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Handling editor: Emory Anderson

ICES Journal of
Marine Science

International Council for
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Conseil International pour
l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2101–2113. doi:10.1093/icesjms/fsu029

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Settlement length and temporal settlement patterns of juvenile cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) in a northern North Sea coastal nursery area

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Bastrikin, D. K., Gallego, A., Millar, C. P., Priede, I. G., and Jones, E. G. Settlement length and temporal settlement patterns of juvenile cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) in a northern North Sea coastal nursery area – ICES Journal of Marine Science, 71: 2101–2113.

Received 27 June 2013; accepted 31 January 2014; advance access publication 11 March 2014.

Knowledge of settlement timing and duration, which has been identified as an important milestone for demersal fish, is critical to understanding population connectivity, relevant to the development of spatially—and temporally—resolved conservation measures, and recruitment variability, as important density-dependent dynamics may take place at this stage. To study the settlement ecology of cod haddock, and whiting, sampling was conducted over spring and summer 2004–2006 at the northern North Sea nursery area. Over 4000 0-group juveniles were collected. Settlement was associated with clear and progressive changes in the prey composition of these juveniles. The size of fish that could be considered settled was estimated as 49 (± 3) mm for cod, 78 (± 4) mm for haddock, and 85 (± 6) mm for whiting. Clear differences in temporal settlement patterns were also apparent. Cod settled in a single pulse lasting about a month (mid-May to mid-June) and initially occupied shallower, inshore waters, whereas haddock settled in one pulse, lasting ~2 weeks (second half of May), favouring deeper, farther offshore locations. Whiting settled much later in the season and over a more protracted period (early June to early August), and their depth preferences also changed over time and with increasing length.

Keywords: 0-group cod, 0-group haddock, 0-group whiting, settlement length.

Introduction

The timing of juvenile settlement on nursery grounds is determined by several factors. The time and duration of spawning by adult fish (Brander, 1994, 2005), water temperature-dependent development of eggs and larvae (Iversen and Danielssen, 1984; Pepin *et al.*, 1997; Brander, 2000; Fox *et al.*, 2003; Geffen *et al.*, 2006), hatch date (Lapolla and Buckley, 2005), ocean currents and tides (Walford, 1938; Kingsford *et al.*, 1991; Shenker *et al.*, 1993; Brander and Mohn, 2004), and distance from the spawning ground (Jenkins *et al.*, 1996), all influence when (and whether) juvenile fish will reach their nursery areas and make the transition to the demersal habitat. According to Hislop (1984) and Coull *et al.* (1998), the spawning period of cod (*Gadus morhua*) in the northern North Sea falls between January and April, haddock (*Melanogrammus aeglefinus*) between February/March and May, and whiting (*Merlangius merlangus*) between March and June/July or February and June. Within a species, spawning time and duration are influenced by maternal characteristics such as size and age (Wright and Trippel, 2009). Prey availability (Bailey and Houde, 1989; Heath, 1992; Brander *et al.*, 2001; Beaugrand and Reid, 2003; Platt *et al.*, 2003), growth (Campana, 1996; Gallego and Heath, 1997; Shima and Findlay, 2002), microhabitat selection (Lough *et al.*, 1989; Tupper and Boutilier, 1995a; Cote *et al.*, 2001), and inter- and intraspecific competition for food and space (Grant and Brown, 1998) can also potentially influence settlement characteristics and subsequent recruitment success.

A significant correlation between indices of larval or juvenile fish abundance and subsequent recruitment was demonstrated by several studies (Helle *et al.*, 2000; Begg and Marteinsdottir, 2002; Jonasson *et al.*, 2009). There is no doubt that processes acting on the pelagic stages of gadoids are important controllers of recruitment success (Hjort, 1914; Walford, 1938; Cushing, 1975; Bailey and Houde, 1989; Sundby *et al.*, 1989). However, the importance of subsequent settlement was also recognized by Campana *et al.* (1989), Tupper and Boutilier (1995a, b, 1997), Campana (1996), and Hüssy *et al.* (1997), who postulated that this transitional stage is crucial for future recruitment and that year-class strength is established at this point. The aim of the present study was to quantify (i) settlement length of cod, haddock, and whiting; (ii) the timing of settlement; and (iii) the duration of this process at the population and individual levels for these three species.

Material and methods

Data collection

0-group cod, haddock, and whiting were collected in Stonehaven Bay (56°58′N 02°11′W), an inshore North Sea nursery area off the Scottish east coast (Figure 1). Stonehaven Bay has a largely sandy seabed, except three natural rocky reefs in the north, perpendicular to the shore, that rise a few metres from the bottom and consist of rough-shaped rocks of various sizes, covered with soft corals and macroalgae. The three reefs are located on the extension of a geological fault running across Scotland known as the Highland Boundary Fault (Craig, 1991). Fish were sampled around these three reefs (sites 1, 2, and 3) characterized by increasing distance offshore (800, 1600, and 2400 m, respectively) and average depths (22, 32, and 42 m, respectively). There were no overlapping depth ranges between sites for the demersal samples collected in 2004. However, there was a depth gradient within each site due to bathymetry, tide, and water level variability. Each site consisted of two different types of substrate: soft sand ("soft" substrate), where demersal trawls and traps were deployed, and rocky reefs ("hard" substrate), where only traps were deployed.

The most intensive sampling took place in 2004 and provided weekly data on changes in the abundance and size frequency in the pelagic and demersal zone at the time of settlement for 0-group cod, haddock, and whiting. Information about spawning time, duration of the pelagic phase (Miller *et al.*, 1963), and time and duration of settlement published previously in the literature determined the initial choice of a sampling period that extended from the end of April until the beginning of September. The limited sampling that was carried out in the 2005 and 2006 sampling seasons provided the basis for comparison of annual abundance fluctuations at the time of settlement and suggested that the 2005 sampling season was a year of higher abundance for all three species.

Samples were collected in the 2004 sampling season by pelagic and demersal trawling. Pelagic sampling started on 26 April and continued weekly from 12 May to 16 August. Demersal sampling commenced on 12 May and continued in 1–2 weekly intervals (mainly weekly) until 31 August. Sampling in 2005 consisted of four demersal and two pelagic sampling events, and in 2006 of two demersal and two pelagic sampling events. Additionally, traps were deployed on five occasions in 2005 and on three occasions in 2006. Pelagic sampling was carried out with a Methot–Isaacs–Kidd trawl and demersal sampling with a fine-mesh demersal trawl specifically designed to catch juvenile fish. Details of gear used in field sampling are given in Demain *et al.* (2011). The dataset from the 2004 sampling season was the most comprehensive and was used to investigate changes in the patterns of catch per unit effort (cpue; hereafter referred to as "density") of 0-group cod, haddock, and whiting in the pelagic and demersal zones over the settlement season. Data from the demersal trawls from 2005 and 2006 were only used for comparison with the patterns observed in 2004.

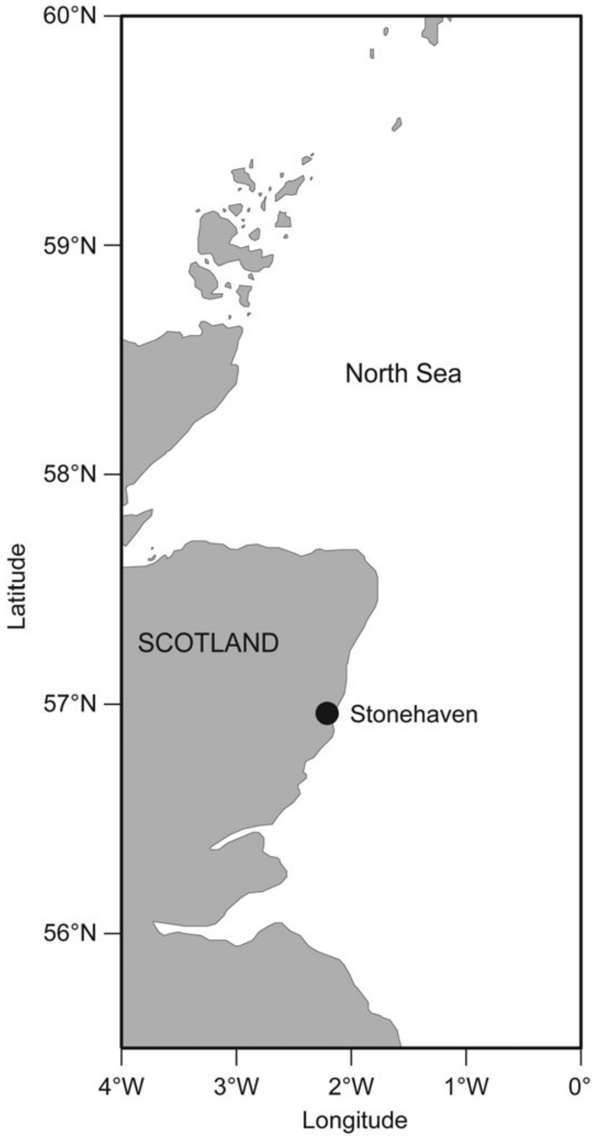

Figure 1. Location of the study site.

Samples were subjected to taxonomic, morphometric, and stomach contents analyses, where relevant; see Demain *et al.* (2011) for further detail. All fish caught were identified to species level and measured. Juvenile cod, haddock, and whiting (from now on referred to as juvenile fish, unless otherwise stated) were preserved for further analyses, and the remaining fish were discarded.

Fish total length (L_T) was measured to the nearest 0.1 mm using digital callipers, and juveniles were subsequently grouped into 5-mm size classes.

Dietary analysis

In total, 2391 stomachs were analysed, of which 1866 were sampled in 2004 and 525 in 2005 (Table 1). Prey items were identified to the lowest possible taxonomic level using the relevant sources (Naylor, 1972; Russell, 1976; Smaldon, 1979; Lowry and Springthrope, 2001; Meland, 2002; Pan, 2004). The resulting taxonomic resolution was considered adequate to provide a general quantitative description of the diet. Highly digested jelly like matter was recorded as "unidentified" and was weighed/counted as a single prey item. Empty stomachs formed an additional category. To provide a quantitative description of the diet, two methods (gravimetric and numerical) were used to analyse 2346 and 1850 fish stomachs, respectively. A comprehensive analysis of the diet was presented in Demain *et al.* (2011).

To determine the length at settlement of cod, haddock, and whiting, prey were categorized as pelagic or benthic, and changes in their relative abundance with increasing size were examined. The relative importance of the pelagic and benthic prey categories was analysed in 5-mm size classes for juvenile fish sampled in all years and by all gear types. Prey types were classed as pelagic or benthic depending on the habitat of the prey item at the time samples were collected, based on information from the literature. For fish species with ontogenetic changes in habitat (e.g. *Ammodytes* spp.), this may introduce some uncertainty, which will be addressed in the "Discussion" section. Prey items of uncertain origin and those impossible to categorize ("unidentified") were grouped into the category "other". Two indices were used to measure changes in relative importance of the pelagic and benthic prey. The first, average weight percentage of each prey type (pelagic, benthic, or other), was calculated as:

$$\bar{W}\%_{xy} = \sum_{j=1}^{n_y} \frac{W\%_{xj}}{n_y}, \tag{1}$$

where $W\%_{xj}$ is the weight percentage of prey type x consumed by fish j. The second, the average number percentage of each prey type (pelagic, benthic, or other), was calculated as above, but by substituting weights by counts.

The settlement threshold was set at the fish length where more than 50% of prey consumed was benthic by weight or number (Bowman, 1981). A binomial logistic regression was fitted to the dietary data, with fish length as a covariate. Logistic regression fits a logistic S-shaped curve to the proportion of prey consumed:

$$\log\left(\frac{P}{1-P}\right) = a + b^{*}\,\text{length}, \tag{2}$$

where a is the regression intercept, b a slope, and P the proportion of prey consumed. From the above model, the length at which the proportion of benthic or pelagic prey consumed equals 50% (l_{50}, corresponding to $P = 0.5$) was calculated. The confidence intervals were estimated from the model and calculated as ± 2 s.e. The same process was followed to estimate l_{50} for pelagic and benthic prey. The settlement interval is presented as the size range between $l_{50\ \text{pelagic}}$ and $l_{50\ \text{benthic}}$.

Table 1. Summary of the number of analysed juvenile fish stomachs collected by two different methods, sampled in 2004 and 2005 (see text for a description of numerical and gravimetric analyses).

Type of analysis	Year	Cod	Haddock	Whiting
Numerical	2004	367	396	1 103
	2005	223	96	208
Gravimetric	2004	361	322	1 023
	2005	128	43	20

Temporal patterns of density and length distribution

To investigating the temporal settlement patterns of 0-group fish, density data from pelagic and demersal samples were analysed. *T*-tests were carried out to test for differences between sampling seasons. For the statistical analysis of the temporal density patterns, only those demersal trawl data collected in the same period in 2004 and 2005 were considered (i.e. between 2 June and 29 July in both years). The 2006 data were not used as they were collected over a very short sampling period and were insufficient for statistical analysis. The explanatory variables tested in density models were site, depth, time (day-of-year), and type of substrates.

The appropriate tool for modelling population density data based on counts which have been collected with a variable sampling effort is a generalized mixed (linear or additive) models (Wood, 2006) using the appropriate probability distribution (Poisson with or without overdispersion and negative binomial) with a log link function and treating the log of the sampling effort as an offset variable. If we denote the underlying density at a given site and time by $D_{\text{site,time}}$, then we can calculate density in terms of the observed counts $N_{\text{site,time}}$ and sampling effort $E_{\text{site,time}}$

$$D_{\text{site,time}} = \frac{N_{\text{site,time}}}{E_{\text{site,time}}}, \tag{3}$$

and, therefore:

$$\log N_{\text{site,time}} = \log D_{\text{site,time}} + \log E_{\text{site,time}}. \tag{4}$$

The generalized mixed model fitted was:

$$\log N \sim \text{site} + s(\text{time}) + \log E, \tag{5}$$

where density has been modelled as a function of "site" and a smooth function of "time", s(time), represented here by day-of-year.

The pelagic dataset consisted of single observations at each site over a series of weeks. Due to the scarcity of data, observations were grouped into two periods (period 1 before 15 June; period 2 after 15 June), where 15 June was the midpoint of the sampling season, and period was treated as a factor. The demersal trawl dataset consisted of weekly observations when sampling took place twice at the same site in close temporal proximity. This is known as cluster sampling and leads to correlation within the pair of samples. The random component of this model allowed the constant and depth effect to differ for each site and sampling week (time).

The best predictive model was selected by forward and backward selection. Significance was assessed by the Akaike Information Criteria (AIC), as follows. The model chosen was the one with the fewest parameters within 2 units of the lowest observed AIC for the dataset in question. This use of AIC for model selection has been discussed by Jones (1993). Significance of individual factors was tested using a Wald test (Agresti, 1990), a multivariate version of *z*-test, which tests for a multivariate difference from zero.

Samples collected by demersal trawls in 2004 were used to investigate changes in the length distribution of 0-group fish over time (day-of-year) on the three sites. These data were analysed using linear regression and analysis of variance (ANOVA). The appropriate distribution for length data is Gaussian (Sokal and Rohlf, 1995; Zuur *et al*., 2007). The assumptions of ANOVA were tested to ensure that independence, normality, and homogeneity criteria were satisfied. The best predictive model was chosen by backward selection from the most complex model, and forward selection from the model including only the global mean. The selected model was the one with fewest parameters within 2 units of the lowest AIC (Jones, 1993).

Results

Foraging habitat and length of settlement

Cod

Cod smaller than 30 mm preyed exclusively on pelagic food items that consisted entirely of copepods, mainly *Temora longicornis* and *Calanus finmarchicus*. From a length of 30 mm, juvenile cod began to feed on benthic prey items, such as *Crangon crangon*, megalopa larvae of crabs, fish (*Ammodytes* spp.), and euphausiids. However, pelagic food still constituted over 75% of the diet weight (84% of prey numbers). Between 30 and 45 mm, the importance of pelagic food decreased; by 50 mm, over 60% of consumed prey weight consisted of benthic animals. At this length, the range of benthic prey consumed expanded to include prawns, shrimps, molluscs, cumaceans, crab larvae (megalopa), amphipods (mainly caprellids and gammarids), and plaice (*Pleuronectes platessa*). The average pelagic food fraction by weight dropped below 1% by the 70-mm length class, and benthic prey constituted >80% of prey weight. The average abundance of pelagic prey by numbers in the 70-mm length class dropped to <10%. Benthic prey numbers were maintained at near 70% or more. Generally, cod over 85 mm did not feed on pelagic prey.

The exceptions were observed only in length classes with small numbers of stomachs analysed (80, 95, 110, 115, and 135 mm), but even then, the decrease in the content of benthic components coincided with increases in unidentified highly digested matter, not pelagic prey.

The changes in relative weight and numbers of pelagic and benthic prey indicate that cod started feeding on benthic prey at 30 mm and by >85 mm, the diet was exclusively benthic. Cod settlement was a gradual process that took place in the length interval 34 (±2)–49 (±3) mm; by 49 (±3) mm (Figures 2a and 3a), as calculated from the logistic regression model, cod juveniles were considered settled.

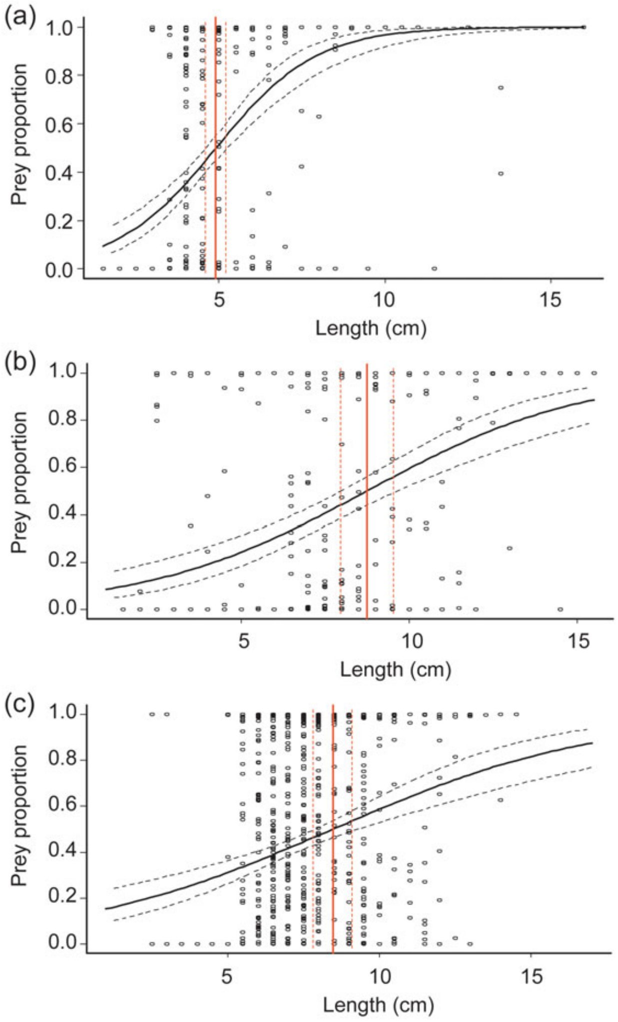

Figure 2. Proportion of benthic prey items by weight in the diet of 0-group cod (a), haddock (b), and whiting (c). Data points represent the percentage of benthic prey in individual fish. Curved solid lines are the logistic regression model fit. Vertical solid lines indicate the estimated l_{50}. Dotted lines indicate ±2 s.e. confidence intervals.

Haddock

Juvenile haddock in length classes <20 mm fed exclusively on pelagic prey (100% of prey by weight and numbers), mainly *Limacina* spp., small copepods, *T. longicornis*, *C. finmarchicus*, and ostracods. In the 20–30 mm interval, the range of crustaceans consumed increased and included amphipods (hyperids), euphausiids (larvae calyptopis and furcila), eggs of invertebrates, zoea larvae of crabs, increasing numbers of copepods, particularly *C. finmarchicus*, *T. longicornis*, and *Pseudocalanus* spp. Insects were also occasionally observed. In this length interval, prey items classed as benthic were encountered in stomachs for the first time. In all instances in this size range, the benthic prey components were *Ammodytes* spp. (in the 30-mm length class, they constituted over 60% of consumed weight) and were found among juvenile haddock sampled by pelagic tows on 24 May 2004. From the 35-mm and above length class, megalopa larvae of crabs, polychaetes, adult euphausiids, and benthic fish (Pleuronectiformes) began to be consumed. In the 50–55 mm length range, there was an abrupt drop in the proportion of pelagic prey consumed. The average pelagic prey by weight dropped from 29.6% in the 50-mm length class to 1.9% at 55 mm and was <3% for all subsequent length classes. The average pelagic prey numbers fell from 50.1% at 45 mm to 25% at 55 mm, to 7.7% by 80 mm, and fluctuated between 0 and 3% at the 100-mm length class. Despite the decrease in the consumption of pelagic prey, an increase in the proportion of benthic prey was not clearly apparent, mainly due to the increase in unidentified stomach content. Particularly in the 55–85 mm length classes, unidentifiable highly digested matter constituted between 50 and 85%

of total prey weight. The majority of haddock with highly digested stomach content were sampled on 15 June 2004, 15 July 2004, and 23 June 2005.

The benthic components constituted over 50% of the diet at 78 (± 4) mm (by numbers; Figure 3b), as calculated from the logistic regression model, the length haddock were considered settled. The proportion of pelagic food in stomachs of haddock decreased below 50% at 29 (± 6) mm (by weight). Therefore, haddock settlement was also a gradual process, which took place in the 29 (± 6)–78 (± 4) mm length interval.

Whiting

Juvenile whiting up to 25 mm fed exclusively on a pelagic diet consisting of *T. longicornis* and small copepods (mainly C1–C4 stages of *C. finmarchicus*). From 20 mm, adult stages of *C. finmarchicus* and *Limacina* spp. were also present in the stomachs. Whiting as small as 25 mm also consumed *Ammodytes* spp. and occasional benthic prey items (polychaetes). From 35 mm, amphipods were also included in the diet and, from 45 mm, crab megalopa. Small copepods and *T. longicornis*, along with larger species such as *C. finmarchicus* and *Candacia armata*, were the most important items in the diet of smaller whiting (up to 45 mm), but they were still present in significant numbers in larger length classes. Pelagic food items constituted over 50% of the diet up to a fish length of 30 mm by weight and 40 mm by number. The one exception, in stomachs analysed by the gravimetric approach, was in the 30-mm length class, where benthic prey constituted 83.3% by weight. Such a large proportion of benthic prey in this length category was mainly due to *Ammodytes* spp., which had been classified as benthic. All 25–30 mm juvenile whiting that preyed on *Ammodytes* spp. originated from a single pelagic tow on 24 May. As whiting length increased further, so did the variety of prey consumed. Larger, heavier prey items such as megalopa larvae of crabs, juvenile crabs, prawns, shrimps, amphipods, cumaceans, and fish made up most of the prey weight. From the 35-mm length class and upwards, the consumption of benthic prey gradually increased to exceed the 50% threshold at 85 (± 6) mm (by weight), as calculated from the logistic regression model. Benthic prey constituted the majority of food of 0-group whiting, by weight and number, from these size classes onwards. An exception was noted at 150 mm, with three fish analysed numerically only, where benthic food content fell to 19.4%. However, this coincided with an increase in unidentified matter, not an increase in pelagic prey.

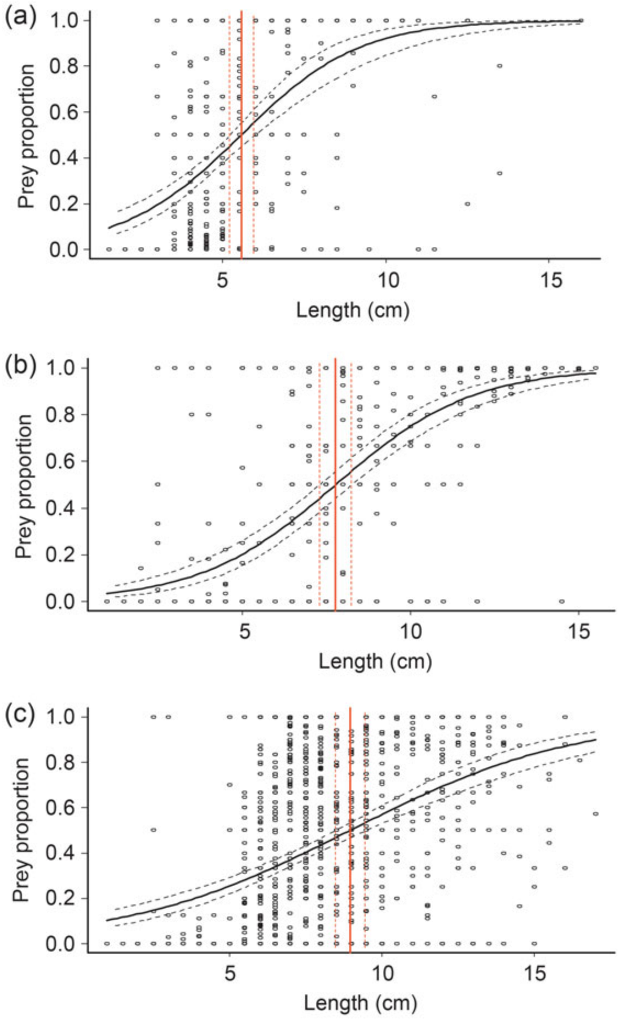

Figure 3. Proportion of benthic prey items by numbers in the diet of 0-group cod (a), haddock (b), and whiting (c). Data points represent the percentage of benthic prey in individual fish. Curved solid lines are the logistic regression model fit. Vertical solid lines indicate the estimated l_{50}. Dotted lines indicate ± 2 s.e. confidence intervals.

Pelagic prey consumption by whiting juveniles dropped below the 50% level at 29 (± 6) mm (by weight). Settlement of whiting was a gradual process that took place in the 29 (± 6)–85 (± 6) mm size interval; by 85 (± 6) mm (Figures 2c and 3c), whiting could be considered settled. Pelagic prey numbers constituted on average over 20% of juvenile whiting prey up to the 115-mm length class, and even in larger length classes, they accounted for a significant amount of prey (only twice below 9% at 130 and 160 mm). In stomachs analysed gravimetrically, the average proportion of pelagic prey by weight fell below 10% by 60 mm (with an exception at 110 mm) and below 1% by 130 mm. This indicates that pelagic prey were many contributors to the juvenile whiting diet through the entire length spectrum. No stomachs were analysed gravimetrically in the 10–20 and 150–170 mm length classes.

Temporal patterns of density and length distribution

Cod

Except 2005, cod were the least abundant demersal juvenile gadoids of the three species of interest. During 2004–2006, 715 cod (15–160 mm) were sampled (Table 2). Cod were first caught in the pelagic samples (Figure 4a) on 17 May (day 138) and last on 14 June (day 166). On the basis of the mixed model analysis, it was concluded that there was a significant time effect on pelagic

Table 2. Summary of the total catches of cod, haddock, and whiting over the 2004–2006 sampling seasons, sampled by all types of gear.

Type of sampler	Year	Cod	Haddock	Whiting
Pelagic trawl	2004	10	152	96
	2005	2	0	2
	2006	0	0	0
Demersal trawl	2004	455	822	2 248
	2005	190	95	209
	2006	1	30	200
Trap	2004	N/A	N/A	N/A
	2005	30	0	1
	2006	27	0	0

cod density (Wald test, $p < 0.05$; Table 3). The density of juvenile cod in the pelagic zone was significantly higher (t-test, $p < 0.05$) before mid-June (first period) than thereafter (second period). Their occurrence in the pelagic zone in 2005/2006 was consistent with the patterns observed in 2004 (Figure 4a). When sampling in 2005 and 2006 took place, no fish were expected to be present in the pelagic zone. This was generally the case, except 27 July 2005, when two 40-mm cod juveniles were captured. Cod were found in the demersal catches from the beginning of sampling (12 May; day 133), a week earlier than in pelagic samples. The density of demersal juvenile cod changed significantly over time (Wald test, $p < 0.05$; Table 4) on all three sites (Wald test, $p < 0.05$; Figure 5a).

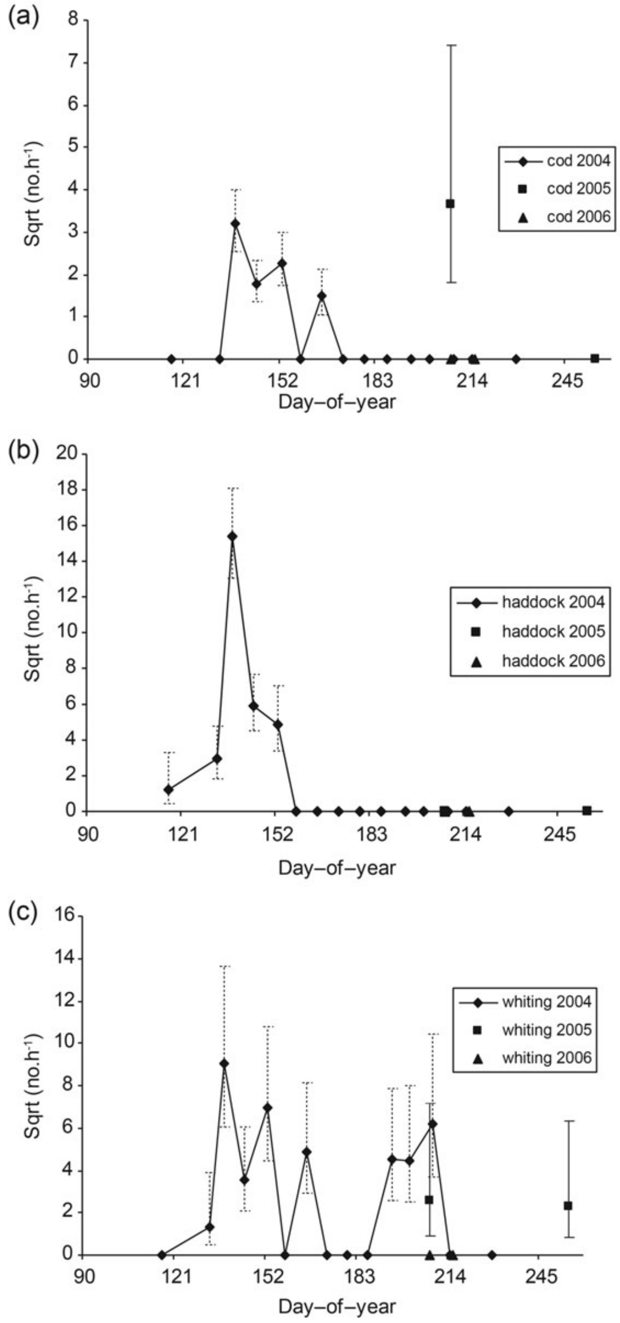

Figure 4. Catches of cod, haddock, and whiting in pelagic trawls in 2004–2006. Data points indicate square root transformed mean number of fish, standardized to number per hour effort, on the sampling day. Error bars indicate ±2 s.e.

The smallest cod was 15 mm long. The length of cod juveniles increased through the season. The maximum length of cod juveniles in the pelagic samples was 40 mm, a length recorded for the first time on 24 May (day 145; Figure 6a). In 2004, cod were the smallest gadoids recorded on the seabed, at a length of 20 mm (Figure 7a). The occurrence of cod in the 20–30-mm length range was quite common in the demersal zone through May and until mid-June. In 2004, in terms of maximum length, cod were the smallest of the three species. From mid-June (day 166), an increase in the minimum and median size was recorded. This coincided with the disappearance of cod from the pelagic catches. Cod reached a maximum size of 100 mm in June, 125 mm in July, and 135 mm in August (over all seasons and all types of sampling gear). The lengths of demersal 0-group cod in 2005 and 2006 were consistent with the patterns observed in 2004, although in 2005, a significantly higher abundance of juvenile cod was recorded (t-test; $p < 0.05$). The length distribution data from 2005 and 2006 obtained by demersal trawling and traps provide additional information to complement the 2004 dataset. Data from 2005 were obtained by trawls and traps, and for 2006 mainly from traps, as only one cod was caught in the demersal trawls (27 July; day 208). The juvenile cod length data for 2005 and 2006, from mid-June (day 174) until the end of sampling (day 251), showed a pattern of gradual increase in minimum and median length (Figure 7a). Statistical analysis of the combined demersal cod dataset showed that juvenile size was positively correlated with time (day-of-year; ANOVA, $p < 0.0001$; Table 5), and it also indicated that there was a gear selectivity effect (traps caught bigger fish than trawls), and a year effect (fish caught in 2005 and 2006 were bigger than in 2004; ANOVA, $p < 0.0001$). Therefore, the combination of all data sources in Figure 7a is just for illustrative purposes.

Most cod settled at the shallowest depth, closest to the shore (site 1) and at the intermediate depth and distance offshore (Site 2) at the beginning of the sampling season, and subsequently the numbers of cod declined on both sites. At site 3, the deepest and farthest offshore, the density of fish also declined over time. The density of cod at this site was significantly lower (t-test, $p < 0.05$) than at the two other sites.

There were significant (F-test, $p < 0.001$) changes in fish length over time and significant differences (F-test, $p < 0.001$) between sites. Cod had a larger mean length at deeper sites (site 2, t-test, $p < 0.001$; and site 3, t-test, $p < 0.05$) than at site 1. The length

Table 3. Model choice summary for pelagic abundance data for cod, haddock, and whiting.

	AIC value			
Model terms	**Cod**	**Haddock**	**Whiting**	**Whiting***
Constant	49.9	127.5	144.1	136.9
Site	51.4	130.0	143.6	139.6
Period	**42.1**	**109.9**	144.3	138.3
Period + site	43.8	112.1	**142.5**	140.6
Period × site	47.8	116.1	140.9	138.9

The best fitting models are indicated in bold. Whiting* was an alternative model for whiting (see text).

Table 4. Model choice summary for abundance of cod, haddock and whiting in demersal trawls.

	AIC value		
Model terms	**Cod**	**Haddock**	**Whiting**
Constant	198.2	283.4	295.5
Site	196.3	265.0	298.9
Depth	196.8	272.2	297.2
Time	171.4	285.1	251.8
s(time)	N/A	N/A	248.3
Depth + time	168.0	N/A	252.2
Depth + s(time)	N/A	N/A	248.0
Site + time	**164.0**	266.0	252.8
Site + s(time)	N/A	**257.5**	247.1
Site:s(time)	N/A	N/A	**243.0**
Site + site:s(time)	N/A	265.1	245.8
Site + depth	196.1	267.0	N/A
Site + depth + time	163.7	N/A	N/A
Site + s(time) + depth	N/A	259.5	N/A
Depth × site + s(time)	162.8	N/A	247.7

The best fitting models are indicated in bold.

distribution, combined with abundance patterns in pelagic and demersal zones, indicates that cod probably settled in a single pulse lasting from mid-May to mid-June.

Haddock

During 2004–2006, 1099 haddock (10–155 mm) were sampled (Table 2). Haddock were the most abundant gadoid juveniles in the 2004 pelagic catch and were sampled for the first time on 26 April (day 117), the earliest of all three gadoid species, at the beginning of the sampling period. Numbers of 0-group haddock subsequently increased, reaching a peak of pelagic abundance on 17 May (day 138). Subsequently, the abundance of haddock declined, and they became absent from pelagic samples by 7 June (day 159; Figure 4b). Time was the only significant effect (Wald test, $p < 0.05$; Table 3), with juveniles significantly more abundant in the first period (t-test, $p < 0.05$). From the patterns of abundance of pelagic haddock observed in 2004, it was not expected to find any haddock juveniles in the pelagic zone when sampling was carried out in 2005 and 2006, as it was indeed the case.

Haddock were present in the demersal catches from mid-May, at the beginning of demersal sampling. The increase in the numbers of juvenile haddock in the demersal catches coincided with their decrease in the pelagic catches. The density of haddock changed over time (Wald test, $p < 0.05$; Table 4), and there were significant differences between sites (Wald test, $p < 0.05$; Table 4). Time was fitted as a smooth function, as the density changes over time were continuous, but non-linear. The plot (Figure 5b) of the predicted changes in the density of 0-group haddock with time at different sites (depths) shows that there was a sudden increase in the abundance of juveniles, particularly in deeper waters (sites 2 and 3), from the beginning of June (day 154) until the peak in abundance at the beginning of July (day 188). It was followed by a decline in the numbers of haddock to an almost constant level from mid-July (day 197). Intermediate depths (site 2) and, to a lesser degree, deeper waters (site 3) seemed to be particularly favoured. The density of haddock at site 1 was significantly lower (t-test, $p < 0.05$) than at the other sites. At the beginning of the sampling season, fish were present at all three sites, but after 6 July (day 188), haddock were caught only at sites 2 and 3. In the 2005 sampling season, a significantly higher abundance of demersal juvenile haddock was observed than in 2004 (t-test; $p < 0.05$; Figure 4b), but overall, results in 2005 and 2006 were consistent with the patterns of abundance of demersal haddock in 2004.

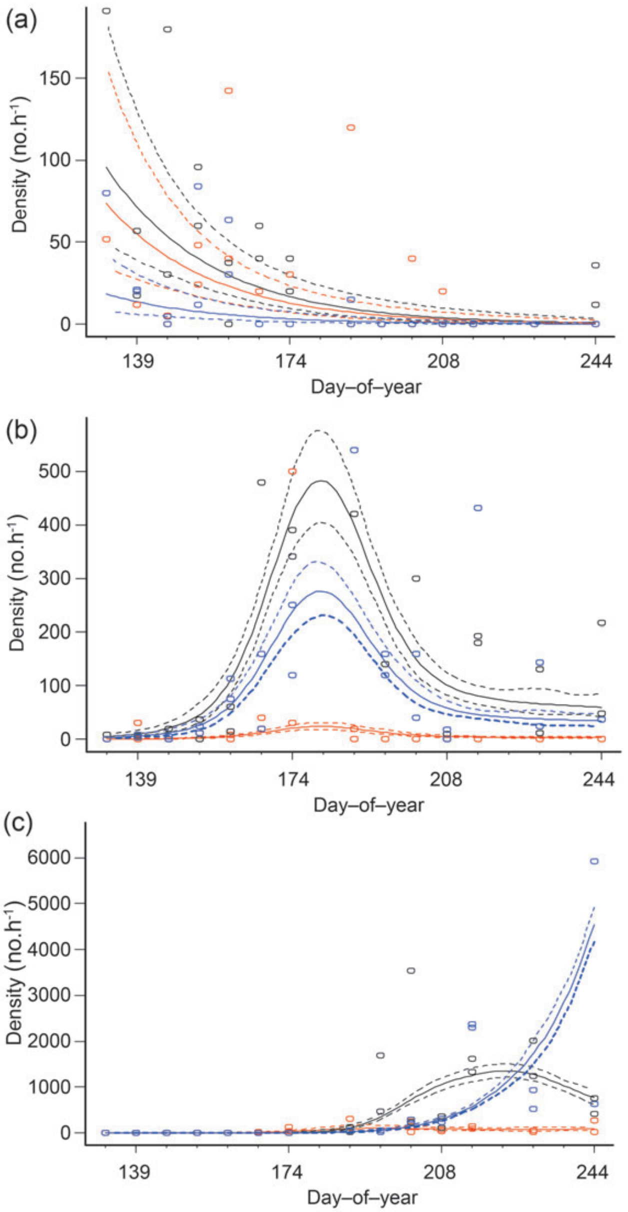

Figure 5. Mixed models outputs of the temporal changes in demersal juvenile cod (a), haddock (b), and whiting (c) density (solid lines) on different sites (site 1, red lines; site 2, black; site 3, blue). Density is expressed as numbers of juvenile fish per hour of sampling effort. Dashed lines indicate ±2 s.e. confidence intervals. Dots represent individual data.

There were significant differences in demersal haddock lengths between different sites (F-test, $p < 0.001$; Table 5). There was also a significant interaction term between site and time (F-test, $p < 0.001$; Table 5), indicating that the pattern of temporal changes in length distribution differed between sites. From the beginning of the sampling season until 6 July (day 188), there was a similar length-change pattern at all sites (Figure 5b). After this

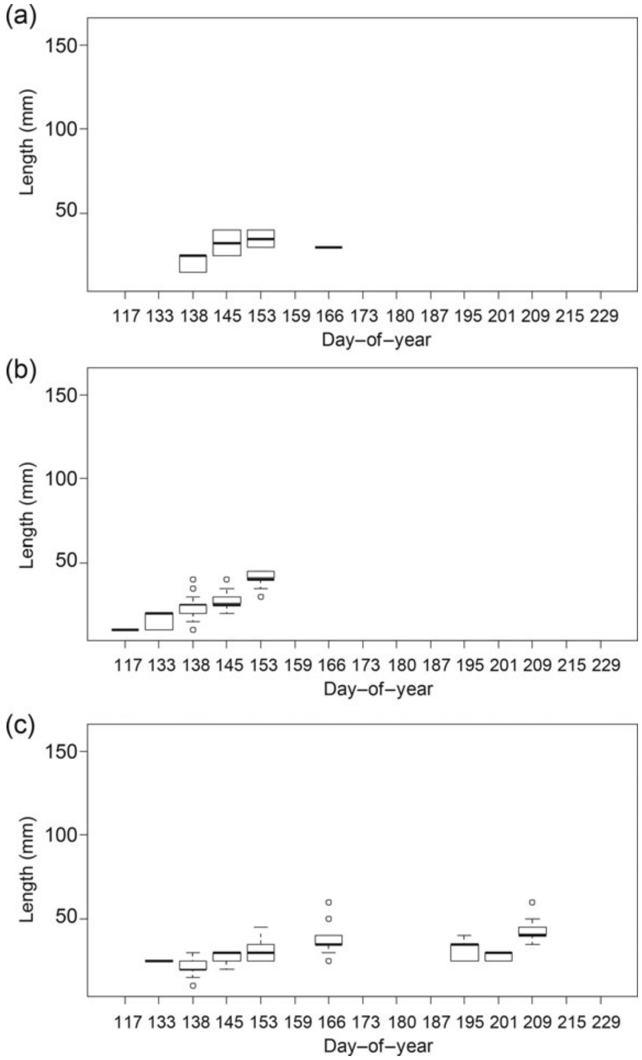

Figure 6. Length distribution of 0-group cod (a), haddock (b), and whiting (c) caught in the pelagic zone in the 2004 sampling season. Boxes indicate the 25th and 75th percentiles of all sizes measured. The upper bars indicate the 10th and the lower bars the 90th percentiles. The thick line indicates the median size. Dots indicate the outliers.

date, fish of increasing length were sampled at sites 2 and 3, but were not present at site 1. Fish at site 1 were significantly smaller than at the other two sites (*t*-test, $p < 0.001$). Fish with the largest mean length were found initially at intermediate site 2 then, towards the end of sampling season, at site 3, the deepest and farthest away from shore.

The smallest pelagic haddock (10 mm) were present in the samples on 26 April (day 117). The length of pelagic juveniles subsequently increased, reaching a maximum of 45 mm on 17 May (day 138; Figure 6b). From the beginning of sampling until 25 May (day 146), the smallest demersal juveniles (30–45 mm) were present in the catch (Figure 7b). From 2 June (day 154), there was an increase in the minimum size of haddock, which continued until the end of sampling. This, combined with the fact that the last pelagic haddock was sampled on 1 June (day 153), suggested that they settled in one pulse that lasted until late May–early June. The length distribution of haddock juveniles in 2005 and 2006 was similar to the patterns observed in 2004 (Figure 7b).

Whiting

Whiting was the most abundant of the three species of interest in all 3 years of study. During 2004–2006, 2756 whiting (10–170 mm) were sampled (Table 2). They were first caught in the pelagic zone on 12 May 2004 (day 133), and the peak in abundance was observed on 17 May (day 138). The last pelagic whiting were caught on 27 July 2004 (day 208; Figure 4c). Exploratory models had indicated that there may be significant time and site effects on juvenile density (Table 3). Small differences between AIC values in all models tested led to further analysis. New model fitting was carried out after removing the most extreme observation (whiting* model in Table 3). This analysis led to the conclusion that there were no significant time or site effects and that pelagic whiting density was constant throughout the area during the sampling period. In the 2005 sampling season, the occurrence of juvenile whiting in the pelagic zone was consistent with the pattern observed in 2004.

Whiting were found in the 2004 demersal samples from the beginning of June, 3 weeks after they were first detected in the pelagic zone. The density of 0-group whiting increased throughout the sampling season (Figure 5c). The patterns of density over time were different among sites (indicated by the interaction between site and time in the model; Wald test, $p < 0.05$; Table 4) and showed a rapid increase in the number of settling juveniles from 8 June (day 160). Until 27 June (day 181), they were present exclusively at site 1 then were caught at all sites. The density of whiting at site 1 from 15 July (day 197) reached a plateau at a level much lower than at the two other sites. At site 2, after 6 July (day 188), numbers of fish increased rapidly, decreased, then levelled off at lower densities than at site 3. Although the increase in the density of whiting at site 3 was delayed relative to site 2, their numbers increased in time to higher levels than at site 2. Overall, juvenile whiting at sites 2 and 3 were significantly (*t*-test, $p < 0.05$) more abundant than at site 1. The abundance patterns of juvenile whiting were consistent in 2004–2006 demersal catches. In 2005, whiting abundance was significantly (*t*-test; $p < 0.05$) higher than in 2004.

Pelagic juvenile whiting ranged from 10 to 60 mm in size in 2004. Between the beginning of sampling and 14 June (day 166), a gradual increase in the maximum size of juveniles was recorded. Throughout the sampling season, small whiting were consistently present in the pelagic samples (Figure 6c). The size of juveniles in demersal samples ranged between 30 and 145 mm. There were significant differences in fish length between sites (*F*-test, $p < 0.001$; Table 5) and a significant interaction term between site and time (*F*-test, $p < 0.001$; Table 5), indicating that length distributions changed with time with a different pattern between sites. Although before 27 June (day 181), small whiting were caught only at site 1, fish caught at the deeper sites 2 and 3 were overall significantly smaller than at site 1 (*t*-test, $p < 0.05$ and <0.001, respectively). The size distribution of whiting, particularly the continuous presence of small juveniles until the end of July, combined with abundance patterns in the pelagic and demersal habitats indicate a protracted population settlement pattern lasting from the beginning of June until the beginning of August. The length distribution patterns of juvenile whiting in the demersal catches in 2005 and 2006 were consistent with the patterns observed in 2004.

Discussion

Similar to other developmental processes, settlement does not occur at a fixed length, but happens gradually and can be influenced by a range of factors such as resource availability and body reserve. In this

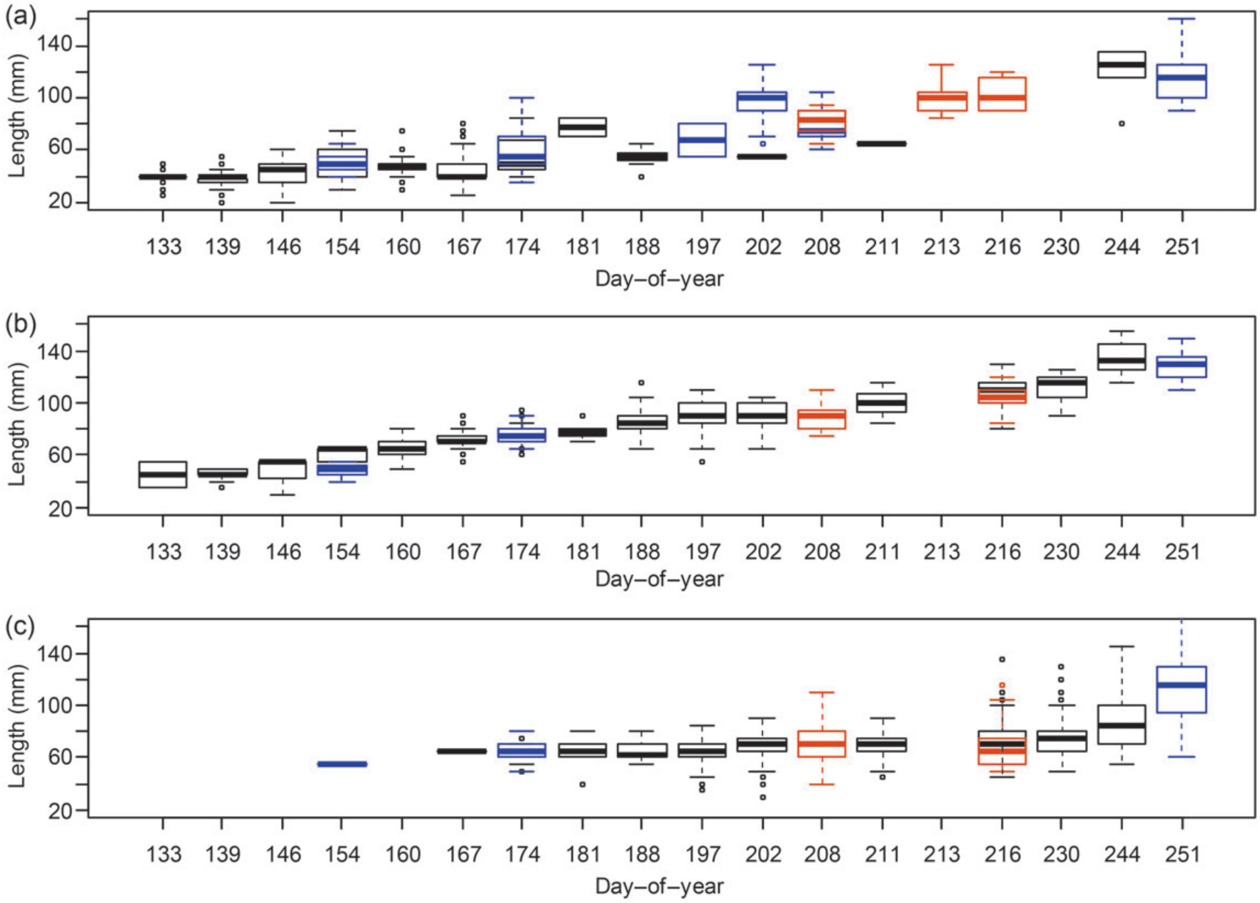

Figure 7. Length distribution of 0-group cod (a), haddock (b), and whiting (c) caught in the demersal zone (combined data for 2004 – 2006 catches from demersal trawls and traps). Boxes indicate the 25th and 75th percentiles of all sizes measured. The upper bars indicate the 10th and the lower bars the 90th percentiles. The thick line indicates the median. Dots indicate outliers. Black colour indicates juveniles caught in 2004, blue in 2005, and red in 2006. On day 208 in 2006, only one cod was sampled by a demersal trawl.

Table 5. Model choice summary for the length distribution of cod, haddock, and whiting caught by demersal trawls in 2004.

	AIC value		
Model terms	**Cod**	**Haddock**	**Whiting**
Constant	1 174.2	3 382.8	8 022.4
Site	1 159.9	3 310.8	7 959.4
Time	1 061.7	2 243.1	7 512.9
Site + time	**1 031.8**	2 239.3	7 513.9
Site:time + time	1 031.2	2 238.8	7 513.2
Site:time + site	1 033.2	**2 235.9**	**7 469.3**
Site × time	1 033.2	2 235.9	7 469.3

The best fitting models are indicated in bold.

study, probabilistic estimates of size at settlement were obtained using a logistic regression technique.

Juvenile cod occurred in the pelagic zone between 17 May and 14 June 2004, but were found in demersal catches from 12 May, suggesting that pelagic cod must have also been present before that date. The very small numbers of 0-group cod caught in the pelagic zone and the absence of juveniles in catches before 17 May were most likely a result of the dispersion of juveniles and their low abundance. The peak in the abundance of pelagic cod was in mid-May, followed by their final disappearance from the pelagic zone by mid-June. Cod were found in the demersal samples throughout the whole sampling period in 2004, with a declining pattern of abundance over time. The drop in abundance may be due to a potential switch to rocky reef habitat by juvenile cod and/or mortality of young settlers. A preference for structured habitat that provides cover from predation was previously reported by Grant and Brown (1998), Lindholm *et al.* (1999 2001), Laurel *et al.* (2003), and Juanes (2007), among others. Attempts at trap sampling on different bottom substrates during the 2004 sampling season were unsuccessful at capturing any juveniles, so no further information is available.

In this study, haddock was the first species to appear (on 26 April), reaching peak of abundance in the pelagic zone on 17 May and finally disappearing from the pelagic zone by the first week of June. This short period of pelagic presence suggests that haddock settled in one single pulse. Coinciding with the decline in pelagic haddock numbers, there was an increase in the demersal zone. This reverse pattern of abundance between the two habitats suggests that settlement in the study area occurred during 1–2 weeks and was completed by the beginning of June. It is not possible to be absolutely certain that there were no haddock present on the seabed before 12 May 2004. An earlier presence of demersal juveniles would imply that settlement had started earlier. However, there was only a single 10-mm specimen sampled in the pelagic zone on 26

April and two demersal haddock sampled on 12 May, suggesting that any significant earlier settlement was unlikely.

After a period of high abundance between mid-June and the beginning of August, the numbers of haddock in the demersal catches dropped. This decline could be due to the movement of growing juveniles into deeper waters (Fulton, 1890; McIntosh, 1897; Klein-MacPhee, 2002), as haddock are generally associated with deeper waters (Klein-MacPhee, 2002), and/or mortality of newly settled juveniles.

Whiting had the most protracted settlement period among all three species investigated. Juveniles were sampled in the pelagic zone from 12 May to 27 July 2004. This was consistent with the general knowledge of the biology of the species, which is known to have an extended spawning season lasting until June–July (Hislop, 1984). Whiting appeared in the demersal catches from 8 June 2004 until the end of the sampling season. The patterns of demersal abundance, pelagic abundance, and length distribution patterns all point towards a very extended period of settlement lasting from the beginning of June until the beginning of August.

The length distribution of 0-group cod, haddock, and whiting in 2004 confirmed the general patterns derived from the abundance data. There was an initial inflow of juvenile cod in the pelagic zone, with the largest cod sampled being 40 mm long. Specimens as small as 20–25 mm were regularly caught in the demersal zone until mid-June. There was an increase in the size of cod with time in the trawl samples, and the largest cod were found at site 2 at intermediate depths. A further increase in size at the deeper site 3 was not observed, but this could be due to the termination of sampling before any changes could be observed, especially since the increasing affinity of cod for deeper waters with age is well documented (Riley and Parnell, 1984; Tremblay and Sinclair, 1985; Keats *et al.*, 1987; Sinclair, 1992; Hessen, 1993; Linehan *et al.*, 2001). The presence of the smallest haddock length class (10 mm) was observed until mid-May in the pelagic zone and, from the second half of May, they were also sampled in the demersal zone (30 mm). The smallest fish were observed in the demersal zone only for the initial 2 weeks of sampling. After that period, a gradual increase in the size of haddock was observed which, together with the absence of juveniles in the pelagic zone, indicated that no new settlers were present. Small new whiting arrivals were recorded in the pelagic catches through most of the settling season, close to the time of their disappearance from the pelagic zone. The demersal fish size distribution showed the presence of small juveniles between the beginning of June and the end of July. This period of settlement agrees with that derived from the abundance data. The presence of 40–60 mm juveniles in the pelagic catches could be an indication that whiting in the area were also undertaking vertical movements after settlement. Whiting settlement took place over a relatively small size range.

The dietary analysis indicated that settlement, defined by the switch from pelagic to benthic prey, was a gradual process that, for cod, occurred at the size range from 34 (±2) mm until final settlement at 49 (±3) mm, a smaller size than previously reported (Daan, 1973, 50–90 mm; Bowman, 1981, >90 mm; Hüssy *et al.*, 1997, 50–70 mm; Lomond *et al.*, 1998, 60–100 mm). For haddock, it occurred at the size range from 29 (±6) mm until settlement at 78 (±4) mm, and for whiting from 29 (±6) mm until it was completed by 85 (±6) mm, also at smaller sizes than previously reported (Heincke, 1905; Robb and Hislop, 1980). Juvenile haddock of the size range 25–30 mm that preyed on *Ammodytes* spp. originated from a single pelagic sample taken on 24 May 2004. This suggests that they were very likely feeding on pelagic forms of *Ammodytes* spp., found in the water column at that time of year (end of May) immediately after metamorphosis, before descending to the seabed (Peter Wright, Marine Scotland Science, pers. comm.; and unpublished data from MSS coastal environment monitoring station in Stonehaven). Therefore, the proportion of benthic prey in these size classes may have been an artefact of the classification of prey items, which did not distinguish between developmental stages of *Ammodytes* spp., as the appearance of pelagic post metamorphic and early demersal stages is very similar. To test for this effect, additional analyses excluding the juvenile size classes that preyed on these *Ammodytes* spp. sizes were carried out. The results showed that, for haddock, the pelagic prey consumption still dropped below 50% at 29 (±3) mm, but benthic prey consumption increased above 50% level at 88 (±3) mm. This range is similar to the original estimate, but suggests a potential underestimate of the maximum haddock settlement size in the original analysis (78 ±4 vs. 88 ±3 mm). An equivalent bias is unlikely to have taken place in the cases of cod and whiting, as the number of juveniles of the relevant size categories that fed on *Ammodytes* spp. was very small and did not affect the statistical outcome.

All the evidence suggests that juvenile cod settle initially close to the shore in shallow waters and move deeper as size increases. This results in at least a partial size segregation, which can reduce cannibalism and increase the chances of survival of 0-group cod (Riley and Parnell, 1984). Although a pattern of increasing numbers in deeper waters coinciding with the observed decline in the shallowest depths was not evident in our data, this in itself does not exclude the possibility of the hypothesized offshore movement without being able to rule out other factors that may reduce numbers farther offshore, such as juvenile mortality. The size distribution pattern observed suggests that, in 2004, there may have been a single pulse of cod settlement lasting 1 month between mid-May and mid-June. This was consistent with the abundance data, where the presence of pelagic juveniles was recorded until mid-June. The subsequent absence of small fish indicates the increasing trend in length distribution was likely due to fish growth. Due to very low catches of cod in July and August, it is difficult to be absolutely certain that there were no more small juveniles settling. However, the absence of juvenile cod from the pelagic catches after mid-June supports the notion that the transition of cod to the seabed was completed by this time. The maximum size of pelagic juveniles, combined with the most common size of small cod in the demersal zone, also supports our conclusions.

Juvenile haddock favoured deeper waters than cod. These depth differences were apparent from the very beginning of the settlement period, when cod favoured the shallower site 1, whereas haddock settled in greatest numbers at site 2 at intermediate depths. Haddock disappeared entirely from the shallowest site from the beginning of July. After an initial increase in abundance, there was a slight decline in the numbers of juvenile haddock towards the end of the season, especially at intermediate depths (site 2). This decline could be due to mortality, a shift to structured habitat, movement of growing individuals out of the study area into deeper waters, or a combination of the above. The size of haddock increased with depth, with the largest fish found at site 3, confirming that larger haddock show an affinity towards deeper waters, farther away from shore (Fulton, 1890; McIntosh, 1897; Klein-MacPhee, 2002).

Throughout June, whiting were found only at the shallowest site. After that time, their numbers increased rapidly at the deeper sites. At the shallowest site, the density of whiting reached a plateau by mid-July at low densities. From mid-July, the highest densities of whiting were found at intermediate depths and, towards the end of the sampling season, on the deepest, most distant site from shore. Small whiting were present in the area from the beginning of June, several weeks after the first cod were caught, and for the first month were found only at the most inshore, shallow site. Throughout most of the sampling season, the largest fish were found at the shallowest site, closest to shore.

The abundance of cod and haddock in 2005 was significantly higher than in 2004, although these results must be treated with caution, owing to the very limited number of samples taken in 2005. These findings were, however, consistent with data from the International Bottom Trawl Survey (IBTS), the Scottish Ground Fish Survey (SCOGFS), and the English Ground Fish Survey (ENGGFS; ICES 2007a, b). They all indicate that, from the estimates of 0-group cod and haddock recorded in 2005 and 1-group cod and haddock recorded in 2006, the 2005 year-class abundance was higher in the North Sea, particularly in the central and northern part, than recent low levels (for haddock about tenfold higher than the average for the 2001–2004 year classes). IBTS data showed the highest numbers of 0-group cod in quarter 3 (July–September) in 2005 since 1998, and the highest numbers of 1-group cod in quarter 1 (January–March) in 2006 since 2002. SCOGFS and ENGGFS data showed the highest numbers of 1-group cod in quarter 3 in 2006 since 2000 and 1998, respectively. According to the IBTS dataset, haddock had a moderate 0-group year class in quarter 3 in 2005 (compared with the high 0-group class abundance in 1999), comparable in size to the 2000 year class, and consistently large numbers of 1-group haddock were sampled in quarter 1 (January–March) in 2006. No notable differences in abundance between the years were recorded in IBTS, SCOGFS, or ENGGFS data for whiting.

Conclusions

Differences in the timing of settlement among the three gadoid species investigated have been identified, with cod being the first species to commence settlement followed by haddock then whiting. There were also considerable differences in the duration of the process. Haddock settled in the Stonehaven area in one short pulse lasting ∼2 weeks, while cod settled over ∼1 month, and whiting over 2 months.

The patterns of length distribution changes through time were different for all three species. Juvenile cod, haddock, and whiting in the Stonehaven area displayed patterns of distribution with depth and distance from shore that led to species and size segregation in time and space, minimizing the potential for competition. The analysis of the feeding ecology of these species showed major differences in dietary composition and little evidence of juveniles preying on each other (Demain *et al.*, 2011), which further supports this conclusion. These factors, taken together, suggest a degree of niche separation which would facilitate the coexistence of these three species.

Settlement of cod, haddock, and whiting appears to be a gradual process which may start with exploratory migrations towards the seabed, during which the juveniles start feeding on benthic prey; as they grow, they increasingly specialize in benthic feeding, although whiting continue to feed in the water column even at larger sizes. A number of authors referred to exploratory migration before actual settlement in the North Sea (Russell, 1922; Bromley and Kell, 1999). The presence in demersal samples of very small juveniles still feeding on pelagic prey is consistent with that exploratory behaviour. The settlement size range calculated for cod in this study points towards a transition to demersal life at smaller sizes than previously reported for North Sea cod (45–65 mm, Robb and Hislop, 1980; 40–80 mm, Bromley and Kell, 1999). Also, the settlement of haddock and whiting observed in this study took place at smaller sizes than those reported in the literature (Heincke, 1905; Robb and Hislop, 1980). Perhaps, a hypothetical tendency to smaller settlement sizes is driven by the same fishery-induced evolutionary process that causes demographic changes in heavily fished populations (Wright and Trippel, 2009). In exploited populations, fish display a large proportion of first-time spawners (Wigley, 1999; Morgan *et al.*, 2003) and, as a consequence, have a narrower spawning season that can affect their reproductive success (Wright and Trippel, 2009) and mature at a younger age (Trippel, 1995). This earlier development may also be found during the early life stages and result in smaller settlement lengths as well. However, to test this hypothesis would require further investigations into the timing and size at settlement on a much wider geographical and temporal scale than in the present study. Alternatively, the differences between these settlement sizes and some of those reported in the literature may be the result of differences in the definition of settlement among authors, and/or more limited datasets.

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Handling editor: Emory Anderson

ICES Journal of Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2114–2126. doi:10.1093/icesjms/fss199

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Review article

Why do assessments of demersal stocks largely ignore habitat?

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Caddy, J. F. Why do assessments of demersal stocks largely ignore habitat? – ICES Journal of Marine Science, 71: 2114–2126.

Received 1 October 2012; accepted 6 December 2012; advance access publication 19 April 2013.

The divergence between most stock assessments and studies in marine ecology is characterized by the low priority usually given to assessing the holding capacity of marine habitats. Habitats of high structural complexity are relatively uncommon in shelf waters, are contagiously distributed, and are damaged incidentally by bottom-towed gear. Structurally complex habitats are used by many demersal fish and crustaceans for predation abatement and as a site for feeding forays. Successive life-history stages typically migrate through several structurally complex habitats which recent studies show often to have fractal properties. One consequence of fractal structures as cover is a rapid reduction of protection from predators with growth in size: migration is the only response possible when further growth of the recruiting age class renders individuals in that habitat vulnerable to predation. A common feature of structurally complex habitats with high vulnerability at size is the occurrence of population bottlenecks. It is suggested that identifying and rectifying shortages of structured habitat, and eliminating habitat bottlenecks, will be effective in stock enhancement. This will require placing strict spatial constraints on the operation of bottom gear. This paper reviews new methods of estimating juvenile predation mortality, including mortality-at-age and mortality-at-life-history stage, which depend on the fractal characteristics of structurally complex habitats.

Keywords: habitat, structural complexity, cover, life history stages, migration, fractals, bottlenecks, natural mortalities.

Introduction

The 1926 study of cod and herring life histories by Johan Hjort (1926) is one of the first contributions to understanding the life history of marine fishes. To this author it was significant, because the conclusions he reached on what was then a new phenomenon are now built into the current paradigm we share as fishery biologists. It is helpful then to re-examine statements which are now truisms such as: "the size of the recruiting year class needs to be taken into account before predicting potential yields", and his conclusion that the new year class is not necessarily a simple function of the size of the spawning population; statements since confirmed by many subsequent studies. This paper tries to follow up on one ancient belief he quoted, namely that changes in holding capacity and productivity of a habitat can influence recruitment variation. To do so, I distinguish between "Environment", the qualities of the water mass of the aquatic environment, and "Habitat", the structural aspects of where fish live and depend on for vital life-history functions. These two characteristics are distinct for demersal/benthic resources, but much less so for pelagic resources (Figure 1). It is also clear that the impacts of fisheries on cover, and of cover on demersal/benthic recruitment, have usually been ignored until quite recently in the literature on fisheries assessment.

Allowing for the impacts of environmental change on fish recruitment is a fairly recent management strategy, even though Hjort made this possibility explicit in his 1926 study of cod recruitment. In the 1960–1970s, for example, approaches to production modelling in support of fishery management sought to eliminate environmental effects by assuming an "equilibrium" between surplus production of resources and fishing effort. This was achieved by an "equilibrium adjustment procedure" (Gulland, 1971) but, later, time-series analyses of several important fisheries (e.g. Caddy and Gulland, 1983) showed that fisheries could be classified into categories that clearly diverged from any sort of equilibrium. Although the driving functions behind annual yield fluctuations rarely distinguished between environment and habitat, there was an incentive to develop empirical dynamic production models which fitted better the real data on

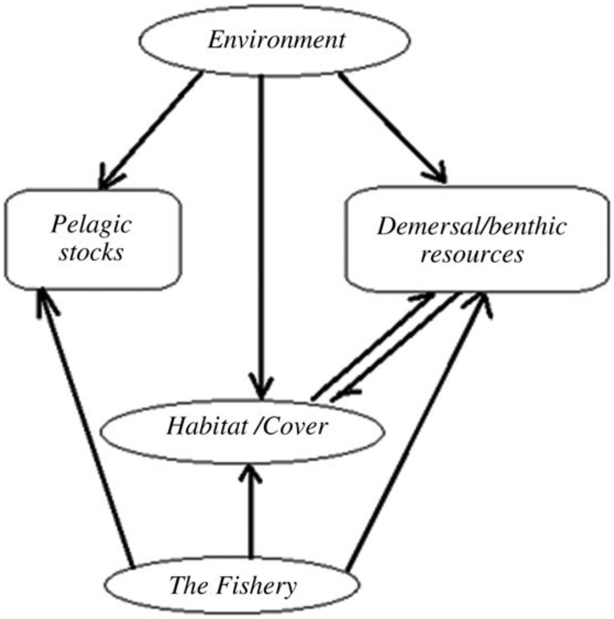

Figure 1. Illustrating the difference between pelagic and demersal/benthic resources where potential impacts of habitat/cover on survival to recruitment are concerned. (Pelagic fisheries impact the stock, but demersal/benthic fisheries potentially also damage the habitat on which the resources are dependent, as do on occasions the resources themselves.)

catch and effort, but still provided no information on the mechanisms behind recruitment variation.

The wide variability of annual recruitment also poses a problem for so-called analytical approaches, which use stock–recruit relationships without explaining the wide scatter of points they typically incorporate. Since there have been few experimental studies on marine fishery impacts with suitable controls, the consequences of changes in the fishery are usually modelled in what is assumed to be an invariant and uniform environment and habitat.

Effects of habitats on recruitment

One aspect that has diverted attention from our understanding of the post-spawning period has been the widespread use of stock–recruitment relationships (SRRs) to "forecast" future year-class strength. SSRs rarely show year-class strength of recruits as a clear function of parental population size. When investigating cod reproduction, Hjort (1926) noted: "it is difficult to avoid the conclusion that the actual quantity of eggs spawned is *not* a factor in itself sufficient to determine the numerical value of a year class". Nor does the SRR gives any explanation for the typically wide annual scatter of points it contains. This relationship only gives us a glimpse into the highly variable but usually unknown events between hatching and when the juveniles reach a potentially exploitable size. In many cases, these events are among the more influential of their life histories. Knowledge of them could suggest specific actions to improve habitat quality, enhance stock size, or reduce negative impacts of fishing. In conclusion, critical events from reproduction to recruitment are not "explained" by the SRR, but it seems likely that the physical structure of the habitat plays a role in the success or failure of recruitment for marine fish, as we know it does for freshwater fish (e.g. Cowx and Welcomme, 1998).

For terrestrial fauna, for example, a threshold of habitat loss of between 30% and 50% is believed to be critical for survival of forest animals (Andren, 1994), irrespective of their state of exploitation. It is not obvious then why habitat fragmentation should not also be critical in the marine environment. Robbins and Bell (1994) documented the fragmentation of sea grass beds, which is often caused by towed gear over a landscape scale, in the Mediterranean. The "gap structure" of cover units that results from dragging gear over vegetated bottoms could be critical, especially for species that migrate from structurally complex inshore nurseries across open sand or mud bottoms to offshore reefs or shelf edges.

Another commonly applied idea assumes that a "dynamic pool" exists which spreads the effect of fishing evenly over the whole stock, i.e. the stock range is "homogenous", and interventions necessarily occur at this level. However, underwater observations show that some habitats and stock components are more vital than others for the survival of economically important species. Fish are usually contagiously distributed, and from detailed studies it seems that key events/locations change in the life history, and must be identified on a GIS landscape scale, rather than on the scale of the unit stock.

Among the phenomena usually missing from assessments of marine fish stocks is how habitat requirements change during the early life history, and how habitat quality declines with destructive fishing. Such information has generally come from direct underwater observations. The renewal of a fish stock in Hjort's words, "is dependent on many factors, *all necessary, and all more or less variable*". As an example, spiny lobster juveniles may pass a critical stage of their early life history in large sponges (Herrnkind *et al.*, 1997); hence, the loss of sponges, due to disease or dragged gear, impacts recruitment through loss of critical habitat. At a still earlier stage, spiny lobsters pass a period where survival is likely to be a function of the health and extent of sea grass meadows (e.g. Bell *et al.*, 2001). Nonetheless, in enhancement work aimed at reducing bottlenecks in life histories, we should consider the high vulnerability of population stages when concentrated in small areas of a habitat critical to a life-history stage.

The extensive use of "casetas" (artificial habitats) on the Yucatan and Cuban shelves undoubtedly increased cover for spiny lobsters in an area of predominantly sand and sea grass beds (Arce *et al.*, 1997) with many lobster predators and little natural cover other than sea grass beds, and led to increased lobster production. Similarly, favourable survival during juvenile cod recruitment is associated with restricted and structurally complex seaweed and cobble bottoms on the Nova Scotian shelf (Keats *et al.*, 1987; Tupper and Boutillier, 1995). Nordeide (1993) also found that stocking fjords with cod juveniles was ineffective in increasing adult populations because suitable juvenile habitat was limiting. Much earlier, the Danish biologist Gunnar Thorson (1957) commented on the shortage of "structured habitat" in the sea. It is therefore reasonable to suppose that this shortage affects recruitment and subsequent survival of recruits.

The "open seabed" is a high-risk environment, and has provided an evolutionary incentive to develop anti-predator behaviours and anatomies. Among these are the radical anatomical adaptations of flatfish and rays, allowing them to hide in bottom sediments, of conchs which develop thick anti-predator shells, the schooling behaviour of juvenile fish in shallow water, and the "queuing" demonstrated by groups of spiny lobsters when crossing sandy bottoms without cover. These examples illustrate the high risk encountered in life on the open seabed without cover.

For bottom-dwelling organisms, recruitment and survival to spawning depend on life-history stages overcoming sequential risks. Survival may be dependent on stage-specific habitat, and its absence may create a "bottleneck" in recruitment supply along the "early recruit → spawner" trajectory. That there are several juvenile stages of many species marked by different food and habitat preferences has been well documented but rarely used in stock assessment. The favoured habitat often changes during development, and Gillanders *et al.* (2003) documented numerous habitat changes by marine organisms in their life histories. These emphasize the need for habitat restoration, and the restoration of spatial linkages between habitats favoured by successive life-history stages (e.g. Lipcius *et al.*, 2008).

Experiments with controls are rare in marine fishery studies, and investigations tend to rely heavily on analysis of fishery time series, often ignoring ongoing changes in habitats. An investigation incorporating habitat preferences requires *in situ* studies, perhaps employing artificial structures installed on the seabed, or spatial comparisons between areas subject to different treatments, as in agriculture research. These effort-intensive approaches are in danger of disruption by towed gear, and, even if this disruption is only a possibility, a lack of control over fishing activities discourages field experiments of long duration. Although a growing number of marine protected areas (MPAs) permit such comparisons, the shortage of quantitative studies on marine habitat and, more to the point, their lack of incorporation into stock assessment procedures, limits the realism of current fishery models.

Effectively there are two separate schools of study of living marine resources: population models based on fishery data or trawl surveys of biomass and age composition; and more detailed *in situ* studies by marine biologists of marine fauna in relation to their habitat. One may speculate that promoting habitat considerations in stock assessment methodologies will require further exchanges between these two fields. In fact, a "habitat complexity" paradigm seems highly desirable as a next step in fishery science, and it could lead directly to bioengineering and habitat interventions. The conclusion of conservationists working on terrestrial species conservation can be recalled—that critical habitat and its continuity in space, and not just species conservation, is the key issue. The current situation of biologists working on fishery conservation resembles that of ornithologists studying bird behaviour without paying attention to the clear-cutting of forests!

Egg–spawner relationships

The SRR in its simplest form assumes equilibrium conditions (Figure 2a). Individual yearly points of stock size are plotted vs. the number of recruits they produce; often incorporating more than a decade of observations. What may have happened to the habitat, or what other environmental changes occurred in the environment during this period, are ignored. Monitoring survival in the larval and post-larval stages needs a dedicated research programme in which habitat requirements and availability, habitat-specific survival rates, and associated migrations are documented. Only for a few species do we have a figure similar to hypothetical Figure 2b which documents habitat-specific survival prior to recruitment to the fishery.

Common marine habitats of the continental shelves

As a broad generalization, on heavily fished continental shelves, most epifauna are sparse but contagiously distributed, with patches separated by wide areas of smooth sediments supporting limited epifauna. This configuration contrasts with the high priority for conservation of cover needed by demersal juveniles to protect them from predation during feeding or migration.

If fishing adversely affects habitats, how will this reduce productivity?

It would not be surprising if the smoothing effect of bottom gear leaves large areas of sedimentary bottom without significant epifauna. Puig *et al.* (2012) recently demonstrated large-scale modifications to shelf and slope environments by trawling. On a smaller scale, Walters and Juanes (1993) illustrated the protective role of cover for small fish when they are not foraging, and explained its trophic significance. That is, motile organisms must remain within a specified distance from cover while feeding, in order to be able to return there when predators appear. The first impact of the absence of cover over extensive areas of flat bottom (perhaps due to past trawl operations) is the additional predation risk this generates for foraging recruits. An additional factor is that it restricts feeding access to only a small proportion of the available food resources in open bottom areas, since anti-predation behaviour requires remaining close to cover while feeding, i.e. the loss of complex habitat has a trophic consequence, namely that "available food" is significantly less available than the total biomass of food organisms present. The likelihood of obtaining large recruiting year classes without access to cover, and hence food, is correspondingly reduced.

Acadjas and other complexities that improve habitats

Knowledge of the role of habitat in increasing fish production (e.g. Caddy and Defeo, 2003) seems to point to habitat modifications that could increase fishery productivity. One methodology used in West Africa illustrates the potential of modifying habitat to offer protection and increase food resources. This functions by "coralling" juvenile fish in an area planted densely with stakes (called locally the acadja; Welcomme, 1972). Juvenile fish in acadjas may even be protected from predators by netting, forming an "acadja-enclos" (Figure 3; Hem and Avit, 1994). One consequence of the acadja methodology is that it leads to early maturity and stunting, given that the quasi-fractal configuration of the planted brush stakes only protects juveniles, not adults. Nonetheless, high densities and productivities of small fish result, without the need for supplementary feeding—they eat the epifauna/flora growing on the stakes. One example from Hem and Avit (1994) illustrates how efficient this methodology is, resulting in yields per hectare much higher than open lagoon habitats. The owners of acadjas in coastal lagoons were accused by conventional "free fishers" of depleting adjacent fishing grounds by aggregating free-living fish in acadjas. The netting enclosure of "acadjas-enclos" was in fact first installed to exclude these fish from entering, in order to satisfy the "free fishers". Only subsequently was it evident that the "acadja-enclos" operators receive their recruits directly through the enclosing mesh, which also excludes escapement of older fish: hence the yield per area increases far in excess of the average productivity of lagoons!

This example illustrates two important aspects of favourable fish habitat, namely the role of structural complexity in increasing cover (e.g. Gotceitas and Colgan, 1989) and how biological productivity is increased by the epifauna/flora that grow on the stakes. Since epifauna/flora biomass increases with habitat complexity,

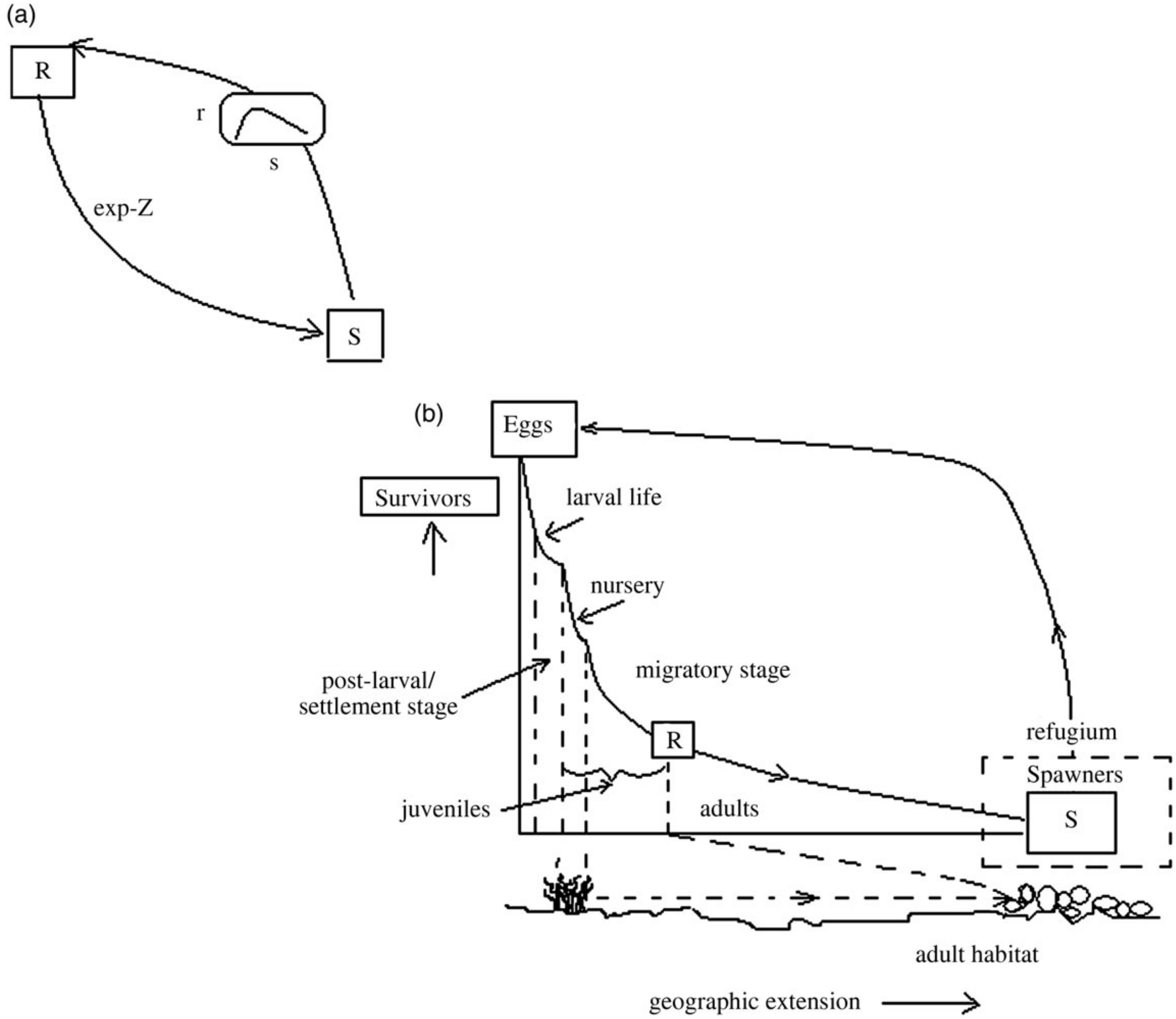

Figure 2. Comparison of the spawner–recruit relationship (a) where survival to spawning is a simple function of fishing and natural mortality, and recruitment is an inevitable consequence of egg production, and (b) where spawner abundance is vital, but spawning also depends on an adult refugium, and recruitment success of the juveniles is subject to sequential risk/bottlenecks during migration between stage-specific habitats (from Caddy, 2008).

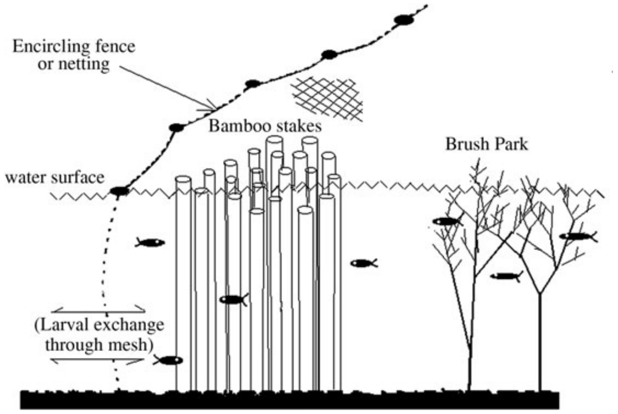

Figure 3. Diagrammatic representation of an "acadja-enclos" used in West African lagoons for fish accumulation—using either brush parks or bamboo stakes (from Caddy, 2007).

juvenile food resources are readily available in acadjas without supplementary feeding. Calculating what configuration and density of structural habitat elements would maximize safe foraging area is a geometric problem which could be tackled by anyone who is interested in applying this mechanism in stock restoration or enhancement.

One mechanism that has been developed to dissuade users of towed bottom gear from working in conserved areas is the "sleeping policeman"; namely, a cement block with metal hooks designed to catch towed gear, installed in sea grass beds or similar structurally complex habitats (Guillén *et al.*, 1994). Marking such structures with warning floats seems an appropriate safety measure.

My definition of habitat follows Peters and Cross (1992): "The structural component of the environment that attracts organisms and serves as a centre for biological activity". Among these structural components is a concept well known to terrestrial ecologists but less so in fish stock assessment—the concept of "cover". This encompasses all characteristics of a habitat, including the following:

(i) The absolute abundance of structural components.

(ii) The relative abundance of different structural components.

(iii) The scale used to measure elements of habitat (Lipcius *et al.*, 1998).

Note that pelagic larvae often settle in complex fractal habitats, but fractal habitats offer progressively less cover with growth in size of the protected organism. Migration will eventually be required to a different habitat type, and migration itself involves a higher risk of predation. Life-history stages (larvae to maturity) may each show different behaviours and habitat requirements, but if stage-specific habitats are limited, this could lead to a "fractal bottleneck" for pre-recruits.

In conclusion:

- Fine sediments dominate benthic habitats. These are low in structural complexity on a macroscale and offer little cover.
- Structural elements are scarce in the sea, are easily damaged by human activities, but may be essential to life-history completion.
- Restoring natural structural elements or adding artificial ones may help restore depleted populations.

Since shortages of specific habitats-at-stage may create bottlenecks, this could reduce recruitment and nullify a stock recovery strategy. For early life-history stages, these "critical habitats" may currently be relatively small areas where habitat components could be protected or restored, or artificial habitats installed, and where foolproof local bans on the use of towed bottom gear can be assured. Examples of soft bottom epifaunal species in deep water, the sea pen and cold-water corals, have both been described as nurseries for red fish (Baillon *et al.*, 2012). Clearly this type of epifauna is very vulnerable to bottom trawling, with predictable consequences.

Habitat complexities in the early life-history stages of demersal and benthic species

The preferred habitats for juvenile fish and invertebrates tend to physical complexity. Red algae, bryozoans, coral reefs, and perforated or crevice-ridden rock surfaces have all been documented as showing fractal distributions (e.g. Burrough, 1981; Williamson and Lawton, 1991). This is characterized by gradation from a few large internal spaces to many more small ones, i.e. inversely, the number of protective structures declines rapidly with growth in size. A simple simulation using the function suggested by Morse *et al.* (1985) for the number of crevices with size in terrestrial vegetation is revealing. When displayed on a fractal surface (i.e. a perforated surface with a fractal coefficient of: $2 < \mathrm{D} + 1 \leq 3$), Caddy and Stamatopoulos (1990) showed that with growth in size, crevice dwelling in fractal habitats leads to predation mortality and hence emigration or stunting. The growth potential of a juvenile forces it into increased vulnerability to predation as larger protective structures in the habitat effectively diminish in number with fish growth, and, in particular, larger cover units are subject to higher competition. This appears to have been the case for the large crevices on the Pedro Bank reefs, as suggested by Caddy (2011) when analysing the data in Munro (1983) with fractal theory in mind. Migration is therefore, in part, structure driven. A high-risk migration to other structured surfaces with larger crevices becomes necessary, unless stunting allows the species to remain in its original habitat and mature and breed at a smaller size.

Structurally complex habitats often have quasi-fractal characteristics

Many structurally complex habitats in nature have been shown to have fractal characteristics. The fractal coefficient of a habitat is often measured along a line or transect (e.g. Burrough, 1981; Bradbury *et al.*, 1984) and values are in the range $1 < D < 2$. However when considering an irregular surface with embedded crevices, the effective dimension must be considered to be in the range: $2 < \mathrm{D} + 1 \leq 3$, as for the coral reefs described by Purkis and Kohler (2008). My proposition is that an ideal habitat for many demersal fish is intermediate dimensionally between a surface and a volume. The term "quasi-fractal" used here is intended to include surfaces where the fractal coefficient may vary spatially, while retaining the general property of fractal habitats that the numbers of spaces between structural elements fall off rapidly with increasing scale.

In quasi-fractal habitats, large crevices are in short supply and this leads to migration or predation

For shelter-dependent animals, competition for the progressively fewer large interstices in a fractal habitat structure inevitably will increase as predicted by fractal theory. Hence, the longer residence times in a given size of crevice for older fish with slower growth (as predicted by a von Bertalanffy curve; Caddy and Stamatopoulos, 1990) further increases competition for the few large habitat units available. This in turn can promote migration and/or a rise in predation. It is reasonable to define such a shortage of habitat when encountered in the growth history as a "fractal bottleneck". We may expect bottlenecks which occur on fractal surfaces to affect the survival of larger fish subject to predation (Caddy, 2011). Other types of bottleneck will occur when there is an abrupt decline in suitable "predator-resistant" habitat with fish size, even if the habitat is not fractal; alternatively, this may occur at the boundary between two types of habitat. It is surprising, therefore, that fish stock modellers make little use of this concept.

Using a fractal array to explore survival of cover-dependent recruits

A number of investigators (e.g. Hacker and Steneck, 1990; Gunnarsson, 1992; Gee and Warwick, 1994) commented on how the fractal nature of many structurally complex marine habitats is particularly relevant for small organisms and juvenile stages of larger, resident species. A study by Morse *et al.* (1985) on how terrestrial vegetation supports insect abundance-at-size had suggested a relationship between the number of cover units on a fractal surface and the number of organisms at size N_L which inhabit it. He formulated this relationship as follows:

$$N_L = k/L^{D+1} \tag{1}$$

where k is a constant, L is the crevice size (and the limiting dimension of the organism inhabiting it), and D is the fractal coefficient.

I simulated how fractal arrays of hole sizes affect survival of inhabitants, using the unpublished "Holes for Windows" software written by C. Stamatopoulos in 1991, which creates perforated surfaces using Equation (1) to disperse predicted numbers of holes-at-size randomly over a surface. These arrays help visualize how the fractal dimension of a habitat determines its holding capacity at size, expressed as a function of the growth rate of its inhabitants. Hole numbers fall off more rapidly with size as the fractal coefficient increases: an array with a coefficient approaching 3 (visualized as a convoluted surface with crevices leading into interior volumes, as in a coral reef), is in fact dominated by small holes (Figure 4). A cohort of small fishes obliged to grow on such a surface rapidly exceed the numbers of suitably sized vacant crevices as they increase in size. We could also expect competition between small adults and the juveniles of larger crevice-dwelling species within a coral fish assemblage. It may be argued that crevice dwelling is not often practised by many demersal fishes. It is common, however, to observe how "free-living" fish aggregate around or in marine vegetation or other complex surfaces; hence, the above argument seems to have some general validity, though, as for all generalizations, many exceptions can be found. It is suggested to use the method described in the following to analyse size frequencies for the rate of decline in frequency-at-size, which can be an indicator of habitat availability and its use as cover.

Low fractal surfaces are more "recruitment friendly"

A surface with a low fractal coefficient, or a natural surface supplemented artificially with larger holes, will facilitate a much less restrictive regime for growth and survival of larger cover-dependent organisms than those with a high fractal coefficient *D*′ which are ideal habitats for post-larvae but promote subsequent migration. It seems possible that migration will be initiated by a predator attack on an individual of close to the maximum size for which the present cover is an effective anti-predator device.

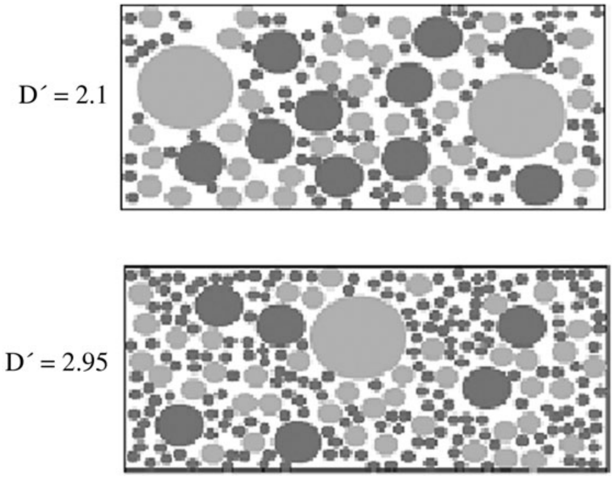

Figure 4. Illustrating how the numbers of "cover units" for organisms of a range of sizes decline with size on surfaces corresponding to two estimates of the fractal coefficient *D*′ (from Caddy, 2007).

Supplementing a habitat with large interstices should be useful for enhancing spawning stocks

Competition for large crevices in artificial reefs, according to Polovina (1991a, b), effectively concentrates larger bottom fish, making them vulnerable to overfishing. This is another way of saying that for larger fish, suitable shelter from predators in adjacent benthic environments is relatively uncommon (Bohnsack, 1989). Also relevant here are observations by Beck (1995) showing that larger boulders are used by stone crabs to hide under while moulting, and their absence in some bays stunts the growth of local crab populations. Auster *et al.* (1996), Caddy (2007, 2011), and Brown *et al.* (2010) argued that structurally complex shelter is rendered scarce in most flat sedimentary environments by swept-bottom fishing gear. Langton *et al.* (1996, 1999), and later, Kaiser *et al.* (2003), raised the need for fishery management to recognize the importance of conserving essential fish habitat, and Cross *et al.* (1997) began considering how to classify it.

Geometrically speaking, there is more "space" available for small than large organisms in fractal cover (Morse *et al.*, 1985), and a method was proposed in Caddy (2011) for identifying bottlenecks from plots of log-size frequencies of resident fish. If a habitat used as cover displays fractal characteristics (see, for example, Burrough, 1981; Bradbury *et al.*, 1984; Bell *et al.*, 1991; Li, 2000), it is postulated that the size frequency data of the inhabiting organisms may be used to determine the value of a scaling quotient of the habitat, *Q*. This measures the mean rate of depletion in numbers-at-size over a segment in a logarithmic size frequency. Consider two crevice sizes that can just accommodate fish of lengths L_1 and L_2, respectively: the limiting ratio of individuals resident there [Equation (2)] is postulated to be related to their size by:

$$N_{L2} = N_{L1} \times (L_1^{\,Q}/L_2^{\,Q}) \tag{2}$$

This relationship can be fitted over close to linear segments of a species log-size frequency to find values of *Q* for that segment (Figure 5). Expressed as $\ln\,(N_{L2}/N_{L1}) = \ln\,(L_1^Q/L_2^Q)$, Equation (2) is equivalent to an instantaneous depletion rate per centimetre increase in fish size. In some restricted circumstances (in the

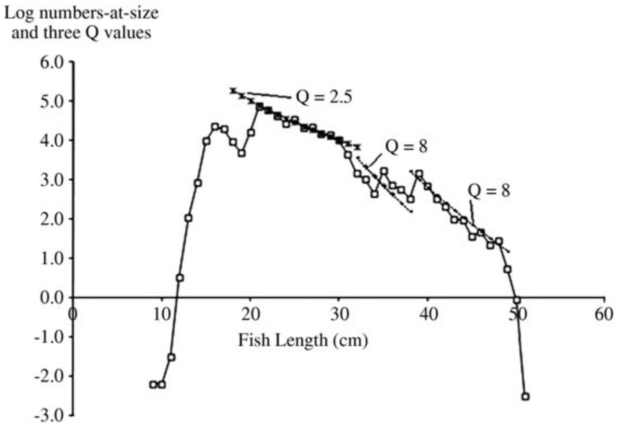

Figure 5. A combined log frequency plot for 15 reef species from Munro (1983), with fittings of the values of Q to three length segments.

absence of fishing or migration), it could also provide a rough measure of the fractal coefficient of the surface, as well as broadly reflecting the apparent mortality rate of resident fish.

Effects of migration, predation, or fishing cannot necessarily be separated based on size frequency declines alone

For unfished resident stocks, the value of Q may reflect habitat availability for populations without cover from predation. However, if fishing mortality or migration are added to the habitat constraint, size frequency analyses will yield Q values potentially much higher than the maximum spatial dimension 3: hence Q no longer has a dimensional significance. Where fractal processes are the main constraint on abundance-at-size, and predation mainly occurs outside cover but neither migration nor fishing mortality apply, values of $Q \leq 3$ could reflect the fractal dimension of the habitat surface available for cover over that size interval.

In a study of data from Munro (1983) for an unfished population of Jamaican reef fish, Caddy (2011) found evidence for 12 species from fish trap samplings where the numbers of fish at size [body height calculated from Fischer (1978) as the limiting body dimension] declined log-linearly at $Q \leq 3$ until a mean body height of 12.5 ± 3.5 cm was reached. Above this size, the rate of decline increased sharply to $Q \geq 8$.

Taking into consideration Munro's comments on the relative scarcity of complex reef cover and the high abundance of sharks on Pedro Bank, this supports the idea that predation rises steeply once reef fish have problems finding cavities larger than ~12 cm or so in height on the reef. Of course this is an adventurous deduction without data on reef crevice sizes, but seems a reasonable one, and is suggested by Munro's excellent dataset which is one of the few available for an unfished marine population. In fact, the combined log plot for 15 species (Figure 5) supports the deduction that all species occupying a common habitat were subject to the same constraints in the face of high predation pressure.

Reanalysing size frequency data from Munro's virgin population, Caddy (2011) found individual scaling coefficients Q for quasi-linear segments of log-size frequency plots. For smaller reef fish subject to predation, trends in log numbers-at-size were close to linear, with $Q \leq 3$, suggesting a fractal expectation for the reef surface/volume their size group inhabited. For larger specimens, steeper declines in numbers-at-size suggest that for them, cover was limited, and predation or migration was occurring well before the maximum size for the species was reached.

I conclude this section by briefly considering a species (*Raja clavata*) that is not dependent on complex cover (Figure 6). A very low value for juvenile Q confirms this; although I would be speculating to suggest why Q reaches a very high value for these animals once over 90 cm (migration or fishing mortality?).

Thus, a shortage of structurally complex elements in the natural environment may expose larger fish to predation (see Walters and Juanes, 1993). This may occur when feeding and predation are more intensive beyond the boundary between structurally complex habitats which provide shelter, and the surrounding flat, sedimentary habitats where foraging and predation often take place. This conclusion stems from numerous field observations (e.g. Sale, 1978; Shulman, 1985; Hixon and Beets, 1989; Holbrook and Schmidt, 2002; Bologna and Heck, 2002).

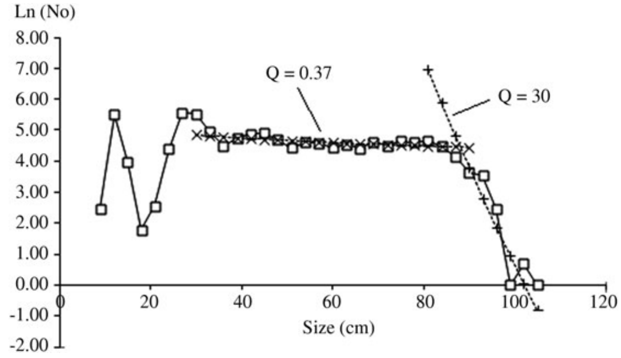

Figure 6. Size frequency plot for *Raja clavata* in the North Sea, from Shepherd (1987), with Q values calculated for two segments.

A typical demersal/benthic life-history displacement

An idealized "epifaunal unit" has progressively finer branchings where "hiding places" and surface areas for growth of food organisms both increase with structural complexity as a function of fractal geometry (Mandelbrot, 1977). A fairly typical life-history trajectory is a migration from a nearshore finely branched nursery or a complex quasi-fractal habitat, passing across open sediment surfaces, to an offshore habitat where "live bottom" or boulders/caves/outcrops offer larger shelters for adult organisms (Figure 7).

Testing for habitat availability in nature

The "Fractal sampler" proposed by Caddy and Stamatopoulos (1990) is a structure with known numbers of crevices of different diameters, whose individual occupancy rates should be controlled at intervals by divers. A high occupancy rate at size implies that holes for this size of organism are scarce in the surrounding area. A similar structure was used by Beck (1995) to explain size distributions of stone crabs in Florida bays; size composition of local populations was found to be a function of the size of crevices under the range of boulder sizes locally available.

Sixteen reef fish species were sampled by Munro (1983) before commercial fishing began on Pedro Bank. These showed similar steep trajectories in the rate of decline of log numbers with size, despite wide species variations in the von Bertalanffy growth coefficient K and natural mortality rate M (Figure 5). Together with the analyses just reported, this suggests that the demography of unexploited reef fish is largely a function of their common habitat rather than simply an expression of different species growth and mortality rates as implied by simplistic parameter analysis.

Different modelling approaches to early life history mortality

A new paradigm comes from working in situations where the old one clearly no longer applies. In the 1980s I was assessing Mediterranean fine-mesh trawl fisheries where the "constant M" approach was evidently inappropriate, since harvesting begins with 0+ to 1+ age groups for which M = 0.2 was improbable! From the limited literature elsewhere, M-at-age for these early age groups is of the order of 0.8–1.5+ annually, and a steep decline with age nullifies the conventional assumption of Beverton and Holt (1957) of "constant M". Their assumption

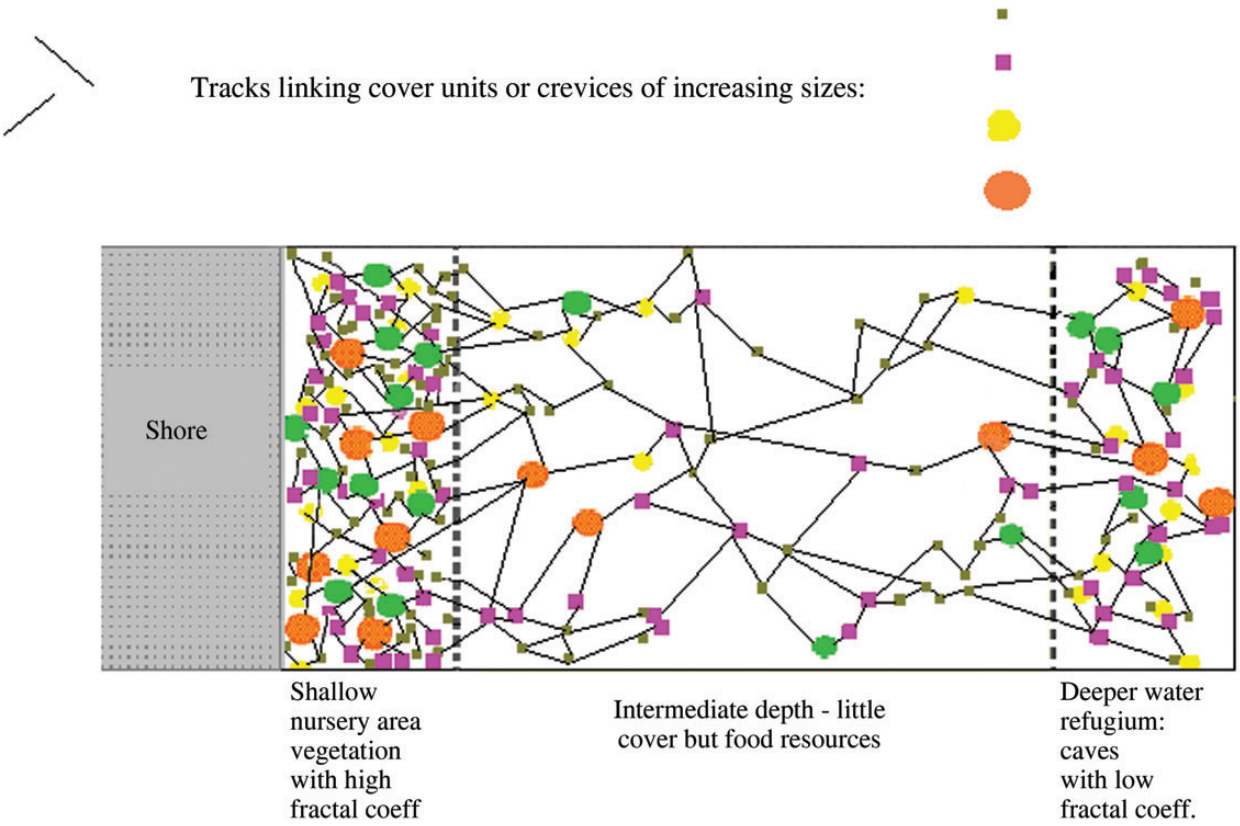

Figure 7. Diagrammatic representation of inshore→ offshore life-history displacement in search of suitable cover resources of the appropriate size (from Caddy, 2007).

was a reasonable one in the North Sea immediately before and after the Second World War, at a time when larger fish were targeted. However, when juveniles and smaller species are the object of fisheries, as they are in the Mediterranean and many tropical areas, this assumption is inappropriate.

Three approaches to generating rapidly declining juvenile M-at-age were investigated which all show similar trajectories for M-at-age.

An empirical fit to data on M-at-age

The size of small fishes in the stomachs of predators within the ICES area implied a high natural mortality of pre-recruits due to predation (Figure 8). By the time maturity approached, M had declined rapidly to a plateau: (i.e. the "constant M" hypothesis may still be a reasonable approximation for adults that are not shelter dependent).

The function: $M_t = A + B/t$ (Caddy 1991) gave a satisfactory fit to data on M-at-age from MSVPA (multispecies VPA) studies in the North Sea (Figure 8).

When used in yield/recruit calculations, it was evident that this "reciprocal M" trajectory reflects the loss of many juveniles due to predation, possibly including an indirect mortality component after passing through the trawl (see Caddy and Seijo, 2011). Whatever the causes of mortality, few of these recruits survive to contribute eventually to yield as maturity approaches, which is what the "constant M" yield/recruit model assumes. That is, the advantages of a mesh size increase are much less than expected with the "reciprocal M" assumption than with constant M-at-age.

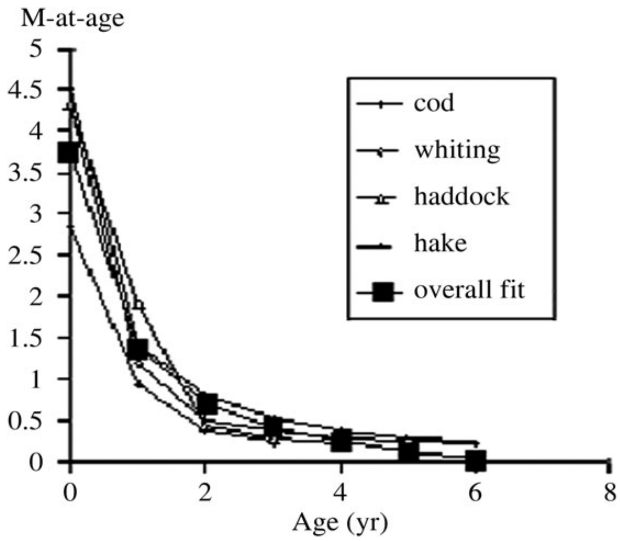

Figure 8. Comparing M vectors with age from the North Sea MSVPA experiment for cod, whiting, and haddock (data from Sparholt, 1990) with an overall fit to the data by the equation $M_t = A + B/t$ (squares).

Conserving the few individuals which reach maturity was evidently the top priority in the Mediterranean, but where are the adults? Certainly mature specimens of large species such as hake are uncommon in the inshore trawl fishery. This question led to the "refugium" hypothesis, which is supported by the early work of naturalists such as Doumenge (1966), who assumed that the few survivors to maturity are in the deeper, rocky, and untrawlable areas of the shelf edge.

A fractal model of M-at-size (Caddy, 1986, 1991)

Structural complexity allows more "spaces" for small than for large organisms in fractal habitats, as described earlier. Habitats with high fractal coefficients make good nurseries for small post-larvae, but low fractal coefficients favour larger organisms (Figure 4). Both types of habitat are present in the marine environment.

A parallel between the increasing spatial scales of fractal theory and the increasing time intervals needed to complete successive life-history stages led to me postulating a "gnomonic" strategy of time division (Caddy, 1996). Successive gnomonic intervals are defined by multiplying a given "seed" interval $t_1 = \Delta_1$ (perhaps the duration of the first life-history stage?), by a constant a, giving $\Delta_2 = a.t_1$ and $t_2 = t_1 + \Delta_2$, and so on, repeating the procedure to obtain a series of progressively longer intervals, until a given maximum age is reached. This strategy was first used to fit intermoult intervals of crustaceans (Caddy, 2003) and then to observed durations of successive life-history stages of different species.

Fractal surfaces imply self-similarity at different scales; thus, for two apertures on a fractal surface of dimensions L_i and L_{i+1}, Morse *et al.* (1985) suggested how holding capacity N_i declines with the size of organisms capable of entering the niches:

$$N_{i+1}/N_i = L_i^{D+1}/L_{i+1}^{D+1} \qquad (3)$$

If animals "under cover" are the only ones that can avoid predators, and the population is unexploited and does not migrate, this equation also becomes an expression for the natural mortality rate of the inhabitants of a fractal surface (Figure 9). The M-at-size that Equation (3) predicts would be relevant to stock assessment of unexploited juveniles dependent on effective cover.

M-at-stage, knowing stage durations

Most fishery theory is expressed in sizes or ages—but is there a role for "life-history stages? Motile organisms with planktonic larvae go through successive stages in ontogeny, each with its physical or behavioural adaptations, and such stages may continue after recruitment. Their duration generally increases in ontogeny, but the mortality rate due to natural causes usually declines with size. It seems reasonable to assume that the total risk of death due to natural causes remains roughly the same for successive stages despite their different durations, but bottlenecks may occur, perhaps due to a stage-specific habitat shortage.

The gnomonic strategy (Caddy, 1996) essentially asks: into what time intervals can a lifespan be divided such that the same risk of death applies in each stage? This reflects the idea that no single life-history stage is favoured by selection over another, and was originally assumed to result in an arbitrary series of intervals of increasing duration. However, this method was used by the following authors to estimate M-at-stages for different species, e.g. jumbo squid (Martínez-Aguilar *et al.*, 2010); pink shrimp (Ramirez-Rodriguez and Arreguin-Sanchez, 2003), red grouper (Gimenez-Hurtado *et al.*, 2009), and venus clams (Arreguín-Sánchez *et al.*, 2012). By comparing gnomonic time durations with development stage durations for a range of organisms, the above-cited authors found that the predicted intervals from Equation (2) for a given life history-stage fitted quite well to the life-history stage durations documented in the literature. Assuming then that the product of stage duration (Δ_s) and M-at-stage (M_s) is roughly constant for different stages, (i.e. $M_s.\Delta_s = \text{const}$), we can arrive at approximations for M-at-stage (Figure 10) if we have an estimate of M for one stage, or if we are willing to simulate from mean fecundity to the survival of one female recruit in an unfished population, following the ideas of Charnov (1993).

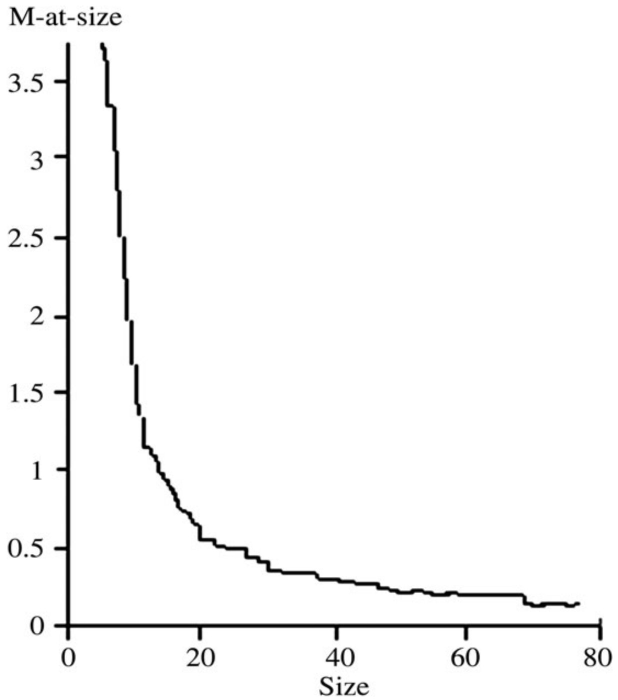

Figure 9. Predicted M-at-size for a life history passed in a fractal environment, if only those in crevices survive.

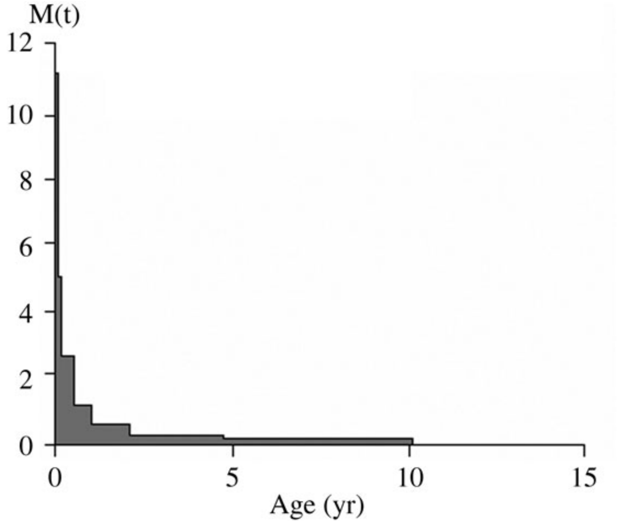

Figure 10. Gnomonic vector of M-at-stage, generated from a "seed" interval of 0.05 year, $a = 1.13$, and a common $M.\Delta t = 1.5$. ($M_1 = 2.75$; $M_{10} = 0.28$). (As the time interval Δt becomes longer following the gnomonic expectation, the mortality rate M declines, but $M.\Delta t$ remains constant.)

Why should successive life-history stages show roughly the same risk of mortality per gnomonic interval? If each stage has its own habitat preferences, this would suggest that genotype fitness is converged on independently by each life-history stage. If so, survival to spawning would not necessarily be optimized by just optimizing habitat for any one stage. If habitat protection of successive life-history stages is a reality, then overall survival to spawning is equally affected by low survival through any earlier stage. Thus, if the survival rate of any stage is anomalously low, it affects population replacement just as surely as a shortage of spawners. The "survival-at-stage" issue and survival "bottlenecks" are therefore relevant to the theme of habitat and cover, and information on preferences of life history-stages should help define any optimal fisheries management strategy.

Bottlenecks

Habitat bottlenecks have been described for a number of species, e.g. stone crabs (Beck, 1995), the crab *Cyrtograpsus angulatus* (Casariego *et al*., 2004), the Caribbean spiny lobster (Eggleston *et al*., 1990), the spiny lobster *Panulirus marginatu* (Parrish and Polovina, 1994), American lobsters (Wahle and Steneck 1991), juvenile fish (Gorham and Alevizon, 1989), coral reef fish assemblages (Hixon and Beets, 1993), and damsel fishes (Holbrook and Schmitt, 2002). Many more examples could be extracted from the literature. One may comment on the high proportion of crustaceans and reef fish in the above list, but this is probably a function of ease of investigation: even temperate zone demersal fish which are "free living" as adults are described as spending a proportion of their time close to rock outcrops, drilling rigs, or a "live bottom" of epifaunal species.

Assuming that the survivors in Figure 11 decline following the M-at-age trajectory discussed earlier, adding one or more bottlenecks, each causing a significant die-off of pre-recruits, will reduce the number of survivors. This will create "unused" habitat and food resources for the few older/larger animals that survive the bottleneck. Then, if the bottleneck reduces density of later stages on more extensive favoured habitats, trophic or habitat constraints will be less severe for the survivors. Habitat restoration as a means of stock enhancement could be undertaken at the bottleneck size without causing density-dependent food shortages (see, for example, Butler and Hernkind, 1997).

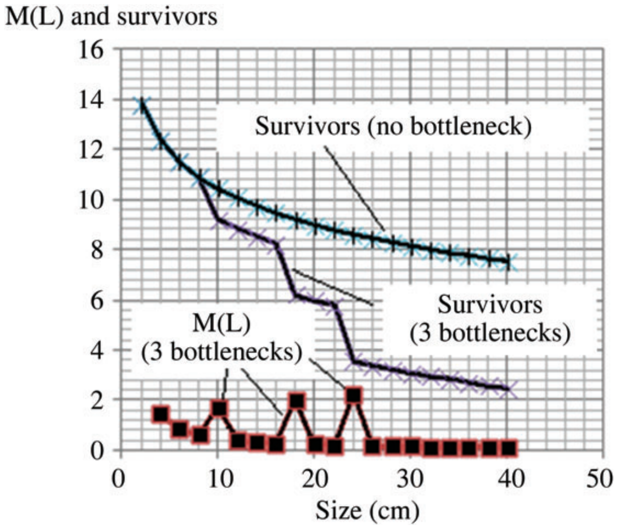

Figure 11. A bottleneck for juveniles may lead to unused adult holding capacity in terms of food and space. In this hypothetical example, three successive bottlenecks cause a dramatic reduction in surviving recruits.

Discussion

Seasonal or life-history displacements are common for motile organisms. Some 30+ different habitat types in the marine environment were distinguished by Gillanders *et al*. (2003). Juveniles moving between them are presumably subject to a higher risk of mortality than when under cover. Habitat structure plays a key role in management of freshwater fish (Cowx and Welcomme, 1998), and this potentially applies to motile demersal marine resources. We may assume that both foraging and migration are high-risk activities when cover is unavailable.

A focus on "cover" is emerging from direct observational studies on "landscape scales" in marine ecology, but the constraint imposed by a shortage of structural habitat is rarely discussed in fish stock assessments. The approach followed here is suited to work on pre-recruit survival on the landscape scales described by GIS techniques, and not exclusively over the area of a unit stock as usually discussed in stock assessment.

For motile marine organisms, at least two rates of natural mortality must apply: one "under cover" and a higher rate "in the open" between stage-specific habitats (Walters and Juanes, 1993), as experienced during "open bottom" feeding or migration. Adult population size in a habitat will be determined by that stage-specific juvenile habitat with the lowest carrying capacity, but on occasions this can be improved on by habitat restoration. Thus, the "bottleneck" is not always on gamete production as usually suggested, or on the trophic supplies available to adults, but primarily on the suitable cover available for different life-history stages.

For an exploited stock, the shortage of cover may be the fundamental constraint that leads to local food shortages. Other related issues are as follows:

- A stock recovery strategy may be effective if it restores vegetation or epifauna, or adds extensive artificial structures.
- For demersal organisms, many life-history interactions occur near the boundary of cover and open bottom.
- Bottlenecks in critical habitat availability may occur for juveniles and nullify earlier spawning success.
- Human activities may also fragment cover and create bottlenecks.
- Mature individuals may require unfished spawning refugia where habitat protection is essential to stock replenishment.
- By analogy with terrestrial conservation considerations, cover continuity could also be important: "vegetated corridors" between stage-specific habitats would improve survival of migrating stages (e.g. Micheli and Peterson, 1999).
- Remediation of damaged critical habitat has the potential to act as a form of stock enhancement.
- Critical habitat conservation measures cannot coexist with the uncontrolled spatial action of bottom gear.

- If we wish our research to result in practical solutions when discussing alternative paradigms, we should ask: do they lead to interesting questions, new avenues for research, or useful applications? I believe the approach described here does so, and, while speculative in part, merits further experimental study.

Closing areas with high relief and abundant epifauna to fishing with towed gear may increase egg production. Installing artificial reefs within MPAs, with their crevice sizes adjusted to the dimensions of mature fish, could create spawning refugia which would supply recruits to adjacent fished areas. Installing acadjas or other juvenile protection devices in reserves could improve survival and feeding of juveniles. Ensuring that migration between stage-specific habitats are to some extent protected by the availability of cover en route seems to be another potential stock enhancement measure (Bell *et al.*, 2001; Caddy and Defeo, 2003; Lipcius *et al.*, 2008). Certainly, taking the time to consider the habitat question in more detail for key species will undoubtedly result in a variety of useful results.

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Handling editor: Frances Juanes

ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2127–2140. doi:10.1093/icesjms/fst203

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Density-dependence can be revealed by modelling the variance in the stock–recruitment process: an application to flatfish

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Archambault, B., Le Pape, O., Bousquet, N., and Rivot, E. Density-dependence can be revealed by modelling the variance in the stock–recruitment process: an application to flatfish. – ICES Journal of Marine Science, 71: 2127–2140.

Received 25 April 2013; accepted 30 October 2013; advance access publication 2 January 2014.

Recruitment success in marine species is mostly driven by the high and variable mortality of first life stages, and the relationships between stock and recruitment are then largely dominated by residual variability. We show that analysing the residual variability may provide insights on the density-dependence process occurring during the recruitment. Following the seminal formulation of Minto *et al*. (Survival variability and population density in fish populations. Nature, 2008), we show that when recruitment is considered as a sequence of a pelagic stage with stochastic density-independent mortality followed by a second stage with stochastic density-dependent mortality, then the variability of the recruitment rate per spawning biomass (RPSB) should be a decreasing function of the spawning biomass. Using stock–recruit data of 148 stocks from the RAM legacy database, we provide a test of this hypothesis by showing that the variability of RPSB is lower for fish species with the higher concentration during juvenile stages. Second, a hierarchical Bayesian model (HBM) is built to derive a meta-analysis of stock–recruit data for 39 flatfish stocks, characterized by a high concentration of juveniles in coastal nursery habitats. Results of the HBM show that the variance of the RPSB decreases with the spawning biomass for almost all stocks, thus providing strong evidence of density-dependence during the recruitment process. Finally, we attempt to relate patterns in recruitment variance to relevant life-history traits of flatfish species.

Keywords: density-dependence, flatfish, heteroscedasticity, hierarchical Bayesian model, meta-analysis, stock–recruitment.

Introduction

Understanding the relationship between the spawning potential and the recruitment (i.e. the stock–recruitment process, hereafter denoted SR) is pivotal for fisheries ecology and fisheries management (Hilborn and Walters, 1992; Walters and Martell, 2004; Houde, 2008). The recruitment process of marine fish species is one of the main drivers of fluctuation in population abundance and critically depends on the high and fluctuating mortality of early life stages (Chambers and Trippel, 1997; Levin and Stunz, 2005; Juanes, 2007; Gallego *et al.*, 2012). In particular, the recruitment rate per unit of spawning biomass (hereafter denoted RPSB) at low population size determines the resilience to exploitation and environmental disturbance (Mangel *et al.*, 2010; Keith *et al.*, 2012; Lee *et al.*, 2012). SR relationships are primordial for estimating biological and management reference points and constitute key components of forward simulations and management strategies evaluation (Punt *et al.*, 2001).

Analysing and modelling SR relationships are both a statistical and an ecological challenge. Several statistical difficulties such as the lack of long time-series of SR data, the poor contrast in stock and spawning potential levels, the presence of observation errors, and/or time correlation in the data hinder the identification of SR relationships and the estimation of associated parameters (Hilborn and Walters, 1992; Hinrichsen, 2001; Needle, 2001; Walters and Martell, 2004). Beyond these statistical issues, the complexity of the mechanisms involved in recruitment variability is also poorly represented by SR models as many factors (e.g. hydroclimate, food availability, competition, and predation) influence the survival at young stages and the recruitment, in addition to spawning biomass. The high and unpredictable fluctuating levels of mortality in early life stages (May, 1974; Koslow, 1992; Chambers and Trippel, 1997; Daewel *et al.*, 2011) reduce or even totally suppress the correlation between the spawning biomass and the subsequent year class

(Hilborn and Walters, 1992; Myers and Barrowman, 1996; Hinrichsen, 2001; Rochette *et al.*, 2012). The recruitment process is thus rarely well described by classical SR models and the residual stochastic variance often largely dominates the signal (Minto *et al.*, 2008).

Motivated by the paucity of data and the difficulty to identify an average signal from a single SR dataset, interest in meta-analysis has grown considerably over the past two decades. Meta-analysis allows to combine information from several fish stocks to help unravelling general patterns that could not be detected with only few data and thus provide a better understanding of the recruitment process (Myers and Barrowman, 1996; Myers and Mertz, 1998; Myers *et al.*, 1999). Open databases such as the RAM Legacy Stock Assessment Data Base, developed by Myers and its successors, have opened new horizons to explore a variety of question related to the recruitment process (Myers and Cadigan, 1993; Minto *et al.*, 2008; Ricard *et al.*, 2011). Although not the only tool for meta-analysis, hierarchical Bayesian models (HBMs) have revealed as a comprehensive and flexible framework for "borrowing strength" between SR datasets (Liermann and Hilborn, 1997; Chen and Holtby, 2002; Prévost *et al.*, 2003; Michielsens and McAllister, 2004; Forrest *et al.*, 2010; Hillary *et al.*, 2012).

In this extensive literature, a large body of work has concentrated on unravelling the expected mean SR relationship to test for the existence of density-dependence such as compensation (Myers and Barrowman, 1996; Hillary *et al.*, 2012) or depensation (Liermann and Hilborn, 1997; Keith *et al.*, 2012). However, although the variance often dominates SR process, relatively poor attention has been paid to examining how the pattern of residual variability in the RPSB can provide insights to the existence of density-dependence mechanisms (Myers, 2001; Minto *et al.*, 2008). According to the seminal concentration hypothesis (Rijnsdorp *et al.*, 1992; Iles and Beverton, 2000), when considering recruitment as a sequence of stochastic process, the variability of the RPSB should be dampened if density-dependence occurs at some latter stages in the sequence. This results in two hypotheses that can be challenged against data. First, when comparing various species, an interspecific pattern showing lower relative variance of the RPSB for species with strong density-dependence regulation during the early life stages should emerge. Second, in the context of SR modelling for one single stock, the variability of the RPSB should be lower at higher stock levels (heteroscedasticity). Based on a meta-analysis of 147 stocks of exploited fish of various species, Minto *et al.* (2008) already inferred the existence of such a heteroscedasticity pattern for many stocks. This contrasts with classical statistical hypotheses, e.g. logNormal or Gamma random variation with constant relative (Jiao *et al.*, 2004), and may have non-negligible influence on the estimates of the RPSB at low stock size or of management reference points such as the maximum sustainable yield (Burrow *et al.*, 2013).

In the present study, we use flatfish species as ideal candidates to elaborate more on these two hypotheses. Flatfish are widely distributed species with high commercial interest (Gibson, 2005), and providing insights on their recruitment process is of major interest for both scientific and management purposes (Iles, 1994). Most of the flatfish are typically nursery-dependent species, whose juvenile stages concentrate on coastal nurseries habitat after a pelagic phase, and thus constitute an ideal case study to analyse how density-dependent regulation in the latter stage can modulate the recruitment variability (Iles and Beverton, 2000). The drift of early life stages (eggs to post-larvae) determines their survival and transport from spawning grounds to nursery habitat (Miller, 2007; Nash *et al.*, 2007). This first phase of the recruitment process is characterized by high and highly fluctuating mortality rates (Van der Veer *et al.*, 2000; Daewel *et al.*, 2011; Rochette *et al.*, 2012), mainly driven by density-independent factors such as temperature effects on growth and survival during eggs and larvae drift. Although the underlying driving process are still under debate, density-dependent mechanisms such as growth limitation and mortality related to food deprivation or increased competition for space occur after metamorphosis and settlement on nurseries (Iles and Beverton, 2000; van der Veer *et al.*, 2000; Le Pape *et al.*, 2003a; Rooper *et al.*, 2004; Juanes, 2007; Johnson, 2007; Nash and Geffen, 2012).

Our objective is to quantitatively assess how the variance of the survival can be analysed to test for the existence of density-dependent regulation at the juvenile stage for flatfish species. We first rely on Minto *et al.* (2008) to highlight why a recruitment process resulting from the combination of two sequential stochastic phases with density-dependence occurring only in the second one results in a dampened variance of the RPSB that varies with stock level. Second, we use 148 stocks from the RAM Legacy Stock Assessment Data Base to test for the hypothesis that the relative variance of the RPSB is lower for flatfish (Pleuronectiforms) than for three other well-documented orders (Clupeiforms, Perciforms, and Gadiforms) for which early life stages are suspected to be less subject to concentration than flatfish. Third, we focus on the SR data series compiled for 39 flatfish stocks and develop a HBM to jointly analyse the 39 datasets to test for the existence of heteroscedasticity in the variance of the RPSB due to density-dependent regulation in the latter stage of the recruitment process. Last, we examined whether some life-history traits suspected to influence the recruitment process (pelagic larval stage duration, level of dependence to restricted nursery grounds) were correlated with the patterns of heteroscedasticity in the RPSB variance.

Material and methods

A theoretical model for the variance of a two-stage recruitment process

As a generic template for the recruitment process in demersal marine fish, we combine an egg/larval pelagic phase between stage S (S being a measure of the spawning stock size) and early juvenile J (just after the end of larval stages), with mortality driven by stochastic density-independent processes, followed by a second phase between J and recruits R where both density-dependent mortality and environmental stochasticity occur. Let us denote α_1 the average survival rate in the first stage with independent and identically distributed (*iid*) logNormal errors e^{ε_1} with $\varepsilon_1 \sim N(0, \sigma_1^2)$:

$$J = \alpha_1 S e^{\varepsilon_1}. \tag{1}$$

Considering that both density-dependence and stochasticity occur between larvae and recruits, the abundance of recruits R is:

$$R = \alpha_2 J f(J) e^{\varepsilon_2}, \tag{2}$$

with $f(J)$ a function (defined latter) modelling how the survival R/J depends on J, and e^{ε_2} *iid* logNormal errors with $\varepsilon_2 \sim N(0, \sigma_2^2)$. Combining the two sequential phases (1) and (2), the RPSB in the log scale is:

$$\begin{aligned}\log(\mathrm{RPSB}) &= \log\left(\frac{R}{S}\right)\\ &= \log(\alpha_1\alpha_2) + \log(f(\alpha_1 S e^{\varepsilon_1})) + \varepsilon_1 + \varepsilon_2.\end{aligned} \tag{3}$$

Considering that the random processes during the two stages are independent, the variance of log(RPSB) is:

$$\begin{aligned}\mathrm{var}(\log(\mathrm{RPSB})) = \sigma_1^2 + \sigma_2^2 + \mathrm{var}(\,\log(f\,(\alpha_1 S e^{\varepsilon_1}))\\ + 2\mathrm{cov}(\log(f\,(\alpha_1 S e^{\varepsilon_1})), \varepsilon_1).\end{aligned} \quad (4)$$

At this step, Equation (4) already shows that even if the two sequential phases have independent random variations, the variance of the whole survival process is not simply additive because, as shown in the covariance term, the stochasticity in the first phase will interplay with the density-dependence of the second stage.

Let us now make the density-dependent function $f(J)$ explicit by introducing the general Deriso–Schnute SR model (Quinn and Deriso, 1999):

$$f\,(J) = (1 - \beta_2 \gamma J)^{1/\gamma}, \quad (5)$$

with $\beta_2 \geq 0$, and the two classical compensatory Beverton–Holt (BH) and over-compensatory Ricker forms obtained as particular cases when $\gamma = -1$ and $\gamma \to 0$, respectively.

Following the same line of reasoning than Minto *et al.* (2008) [using the Delta method to approximate the variance and covariance terms in Equation (4)], var(log(RPSB)) can be approximated by:

$$\mathrm{var}(\log(\mathrm{RPSB})) \approx \left(1 - \frac{\beta_2 \alpha_1 S}{1 - \gamma \beta_2 \alpha_1 S}\right)^2 \sigma_1^2 + \sigma_2^2, \quad (6)$$

which simplifies under the special BH [Equation (7a)] and Ricker [Equation (7b)] cases to:

$$\mathrm{var}(\log(\mathrm{RPSB})) \approx \left(1 - \frac{\beta_2 \alpha_1 S}{1 + \beta_2 \alpha_1 S}\right)^2 \sigma_1^2 + \sigma_2^2, \quad (7a)$$

$$\mathrm{var}(\log(\mathrm{RPSB})) \approx (1 - \beta_2 \alpha_1 S)^2 \;\; \sigma_1^2 + \sigma_2^2. \quad (7b)$$

Equation (6) and particular declinations [Equations (7a) and (7b)] highlight how the variance of the density-independent stochastic phase (σ_1^2) is modulated by the intensity of the density-dependence, here parameterized by β_2 and the shape parameter γ. According to Equation (7a), when considering a compensatory BH density-dependent form, var(log(RPSB)) is a monotonous decreasing function of the stock size S, between $\sigma_1^2 + \sigma_2^2$ and the minimum value σ_2^2. When considering a Ricker form (i.e. with over-compensation), var(log(RPSB)) decreases until $S < 1/\beta_2\alpha_1$, then increases for higher S. As stated by Minto *et al.* (2008), such a domed-shaped relationship is general for over-compensatory SR models such as Ricker or Shaefer. Nevertheless, the pivotal stock value ($1/\beta_2\alpha_1$) is generally rather high, and, for exploited stocks, most of the values of S are likely to occur in the range where the variance decreases with the stock size (Minto *et al.*, 2008).

Even if considering the recruitment process as a sequence of two phases as in Equations (1) and (2) could fit well to many fish species (flatfish in particular), such a two-stage model is over parameterized for classical SR analysis for which no data on the intermediate stage J is available. However, the theoretical construction developed above shows that when considering classical SR models under the hypothesis of LogNormal random variations as in Equation (8):

$$\log(\mathrm{RPSB}) = \log(\alpha) + \log(\,\mathrm{f}\,(\mathrm{S}, \beta, \gamma)) + \;\varepsilon \quad (8)$$

with $f(\cdot)$ the generalized Deriso–Schnute form in Equation (5) and *iid* logNormal errors e^{ε}, with $\varepsilon \sim N(0, \sigma^2)$, the following patterns in the variance of log(RPSB) [in Equation (8)] should be expected.

(i) First, Equations (7a) and (7b) show that the variance should be lower for species (or orders) with concentration mechanisms occurring at a later stage in the recruitment process. In particular, Equation (7a) highlights that when considering a BH form, all things being equal, the higher the density-dependence in the second stage (i.e. the higher β_2), the lower the ultimate variance. The asymptotic minimum values of var(log(RPSB)) is σ_2^2, i.e. the variance of the first phase σ_1^2 is fully dampened by density-dependence.

(ii) Second, when considering the resulting patterns of stochasticity for a single stock, σ^2 should be a function of the stock, as soon as density-dependence occurs in the second phase of the recruitment process (i.e. β_2 is non-null). For realistic parameters and most of the observed stock values, and especially largely exploited flatfish, σ^2 is expected to be a decreasing function of S, whatever the density-dependence form.

Stock–recruit data

The data (Table 1) included 148 stocks: 39 stocks of 17 flatfish species (Pleuronectiforms) and 109 stocks of 44 non-flatfish species (Clupeiforms, Perciforms, and Gadiforms). All data were derived from statistical catch-at-age models (e.g. VPA, XSA, ADAPT) to ensure homogeneity. Most of the SR series were obtained from the RAM legacy database (Ricard *et al.*, 2011). The data from the RAM database was completed with three additional flatfish stocks and by adding the most recent data gathered from flatfish stock assessment reports published by regional working groups. This corresponds to 1237 SR flatfish observations (Table 2), constituting an increment of 15% about suitable flatfish data found in the RAM legacy database (Ricard *et al.*, 2011).

Comparing the variance of the survival process between fish orders

The 148 stocks were included in a first analysis designed to compare the variance of recruitment process between the four fish orders. For each of the 148 stocks, var(log(RPSB)) was estimated independently by fitting BH or Ricker models as in Equation (8) with a simple least-square procedure. No standardization of the data was required, as σ^2 in Equation (8) is independent of the unit of S and R. The estimates of σ were then compared across orders, and a

Table 1. Synthesis of the dataset used for the inter orders analysis (RAM legacy database supplemented by additional data for Pleuronectiforms).

Order	Species	Populations	Observations *total* (min, mean, max per population)
Clupeiforms	9	30	1 052 (16,35,54)
Perciforms	25	33	1 288 (9,39,79)
Gadiforms	10	46	1 518 (12,33,77)
Pleuronectiforms	19	39	1 237 (10,32,55)
Total	63	148	5 095

Table 2. Synthesis of stock–recruitment data (upgraded from the RAM legacy database) and life-history traits for Pleuronectiforms.

					Uncertainty (CV in %)	
Species/stock	**$\text{SPR}_{F=0}$**	**Time-series range**	**Nursery type**	**Pelagic stage duration (d)**	***S***	***R***
Alaska plaice (*Pleuronectes quadrituberculatus*)						
Bering Sea–Aleutian Islands	2.51	1975–2005	2	NA		
American plaice (*Hippoglossoides platessoides*)						
NAFO 3LNO	2.53	1960–2002	4	75		
NAFO 3M	2.77	1988–2006				
NAFO 5YZ	1.40	1980–2007				
Gulf of Maine–Georges banks	2.18	1980–2004				
West Greenland	2.09	1982–1991				
Arrowtooth flounder (*Atheresthes stomias*)						
Eastern Bering Sea–Aleutian Islands	1.56	1976–2002	NA	135		
Arctic	2.47	1961–2004				
Dover sole (*Microstomus pacificus*)						
Gulf of Alaska	0.85	1984–2004	NA	460		
Flathead sole (*Hippoglossoides elassodon*)						
Bering Sea: Aleutian Islands	0.73	1977–2005	NA	NA	5	17
Gulf of Alaska	0.86	1984–2006				
Fourspotted megrim (*Lepidorhombus boscii*)						
ICES 8c9a	0.50	1986–2010	4	NA		
Greenland halibut (*Reinhardtius hippoglossoides*)						
NAFO Subarea 2 and Divisions 3 *KLMNO*	4.34	1975–2010	3	150		
Eastern Bering Sea–Aleutian Islands	3.17	1970–2011				
Northeast Arctic	8.43	1964–2010				
Megrim (*Lepidorhombus whiffiagonis*)						
ICES 8c9a	0.45	1986–2010	4	NA		
Pacific halibut (*Hippoglossus stenolepis*)						
North Pacific	131.27	1996–2012	2	135		
Plaice (*Pleuronectes platessa*)						
ICES IIIa	2.46	1978–2004	2	60	10	25
North Sea	2.23	1957–2011				
Irish Sea	1.58	1964–2008			31	19
Celtic Sea	1.98	1977–2009				
ICES VIId	2.70	1980–2011				
ICES VIIe	2.45	1980–2010				
Rex sole (*Glyptocephalus zachirus*)						
Gulf of Alaska	0.57	1982–2004	4	365		
Sole (*Solea solea*)						
ICES IIIa	1.20	1984–2011	4	45		
North Sea	1.16	1957–2011				
Irish Sea	0.98	1970–2011				
Celtic Sea	1.31	1971–2011				
ICES VIId	1.16	1982–2010				
ICES VIIe	1.19	1969–2010				
ICES VIII	1.91	1984–2010				
Summer flounder (*Paralichthys dentatus*)						
North Atlantic	3.48	1982–2007	1	50		
Winter flounder (*Pseudopleuronectes americanus*)						
NAFO 5Z	1.50	1982–2006	1	35		
Southern New England–Mid Atlantic Bight	1.39	1981–2007			11	
Witch flounder (*Glyptocephalus cynoglossus*)						
NAFO 5Y	1.10	1982–2007	4	240	14	
Yellowfin sole (*Limanda aspera*)						
Bering sea – Aleutian Islands	0.91	1964–2003	2	45		
Yellowtail flounder (*Limanda ferruginea*)						
Cape Cod–Gulf of Maine	1.16	1985–2006	4	105		
Georges Banks	1.44	1973–2007				
Southern New England–Mid Atlantic Bight	1.28	1973–2006				

$\text{SPR}_{F=0}$ is the cumulative biomass produced per recruit over its lifetime in the scenario of no fishing mortality (see text for details). Nursery type is given by decreasing concentration order (adapted from Gibson, 2005), from 4 (strongly nursery-dependent) to 1 (weakly dependent).

multiple comparison Tukey test was used to test for the between orders difference.

A HBM to test for heteroscedasticity in the flatfish recruitment process

A HBM was built to jointly analyse the 39 flatfish SR datasets (Table 2) and to assess the patterns of heteroscedasticity in the variance of the SR process. Based on the theoretical construction (1) and (2), the most parsimonious model in Equation (8) was considered, with a variance of the recruitment process σ^2 considered as a function of the stock size [see explanations below, in Equation (11)]. Each SR dataset, if considered alone, is suspected to provide insufficient information to estimate the variance as a parametric function of S (Burrow *et al.*, 2013). Hence, a hierarchical approach was required to borrow strength between SR datasets.

Data standardization

To make the parameters comparable across stocks (Minto *et al.*, 2008), the SR data series were first standardized so all S and R are expressed in comparable units and ranges across the 39 stocks. To do so, the recruitment data were standardized into the same unit than the stock (i.e. biomass of spawners). The standardization introduced by Myers (2001) was used. It consists in multiplying R by $\text{SPR}_{F=0}$ which is the cumulative spawning biomass produced by a recruit over its lifetime in the scenario of no fishing mortality (Gabriel *et al.*, 1989).

$$\text{SPR}_{F=0} = \sum_{i_{\text{rec}}}^{i_{\max}} \mathrm{e}^{-[M_i(i-i_{\text{rec}})]} W_i \text{Mat}_i, \tag{9}$$

where i_{rec} is the age of recruitment, $i_{\max}$ the maximum age-class, M_i the natural mortality at age i, W_i the mean weight at age i, and Mat_i the proportion mature at age i. Values of $\text{SPR}_{F=0}$ were estimated for each stock, using natural mortality, weights-at-age, and maturity-at-age estimates from stock assessments reports.

All series of S were then scaled with a maximum at 1, as in Minto *et al.* (2008), but recruitment series were standardized by the same factor than the stock, i.e. the maximum S for each stock. While the choice of standardization does not affect variance estimates, standardizing both S and R by the same constant [max(S)] preserves the R/S ratio in the original data, and thus allows for comparison of stock–recruit parameters such as the maximum RPSB rate (or the maximum lifetime reproductive rate; Myers, 2001). From now on, for clarity purposes, S, R, and RPSB denote, respectively, the spawning biomass, recruitment, and RPSB after standardization.

Hierarchical Bayesian model

The BH [Equation (10a)] and Ricker [Equation (10b)] models were tested as two special cases of the generic model in Equation (8). Both models were reparameterized in terms of α, the maximum RPSB rate and K, the maximum recruitment ($K = \alpha/\beta$ and $K = \alpha/\beta e^1$ for the BH and Ricker forms, respectively):

$$\log(\text{RPSB}) = \log(\alpha) + \log\left(\frac{1}{1 + aS/K}\right) + \varepsilon \sim N(0, \sigma^2), \tag{10a}$$

$$\log(\text{RPSB}) = \log(\alpha) - \frac{\alpha}{Ke^1} S + \varepsilon \sim N(0, \sigma^2). \tag{10b}$$

Table 3. Model parameters and prior distributions in the configuration with all parameters (η_1, η_1, α, K) stock-specific.

Parameter	Description	Prior distribution
Hyperparameters		
μ_{η_1}	Mean η_1 across stocks or species (according to model structure)	N (0,20)
$\mu_{\eta 0}$	Mean η_0 across stocks	N (0,20)
$\mu_{\log\alpha}$	Mean log α across stocks	N (0,10)
$\mu_{\log K}$	Mean log K across stocks	N (0,10)
σ_{η_1}	Standard deviation of η_1	U (0.01,20)
$\sigma_{\eta 0}$	Standard deviation of η_0	U (0.01,20)
$\sigma_{\log\alpha}$	Standard deviation of log α	N (0.01,3)
$\sigma_{\log K}$	Standard deviation of log K	U (0.01,3)
Parameters at the stock level		
η_1	Heteroscedastic coefficient	$N(\mu_{\eta_1}, \sigma^2_{\eta_1})$
η_0	Density-independent variance component	$N(\mu_{\eta_0}, \sigma^2_{\eta 0})$
α	Slope at origin of $S-R$ fits	log $N(\mu_{\log\alpha}, \sigma_{\log\alpha})$
K	Asymptotic R value of $S-R$ fits (carrying-capacity)	log $N(\mu_{\log K}, \sigma_{\log K})$

This parameterization allows comparing parameters between the two particular forms. This is important for Bayesian models as it allows for the definition of common priors, which is a key issue for model selection (Lawrence *et al.*, 2013; Pulkkinen and Mäntyniemi, 2013). The variance σ^2 in Equations (10a) and (10b) was reparameterized as a function of stock size S (Minto *et al.*, 2008):

$$\sigma^2(S) = \exp(\eta_0 + \eta_1 S), \tag{11}$$

where η_1 scales the magnitude of heteroscedasticity. Fixing η_1 to 0 gives the classical widely used logNormal errors with constant variance.

Hierarchical structures were set on parameters (α, K, η_0, η_1). Parameters (α, K, η_0) were considered as stock-specific and exchangeable across stocks (all other models considering those parameters pooled by species or common to all stocks had very poor fit to the data). Parameter η_1 was considered either stock-specific or species-specific (17 species for 39 stocks; Table 2).

All parameters were given weakly informative prior distributions (Table 3) in the sense of Gelman (2009), i.e. they let the data speak while being strong enough to exclude unrealistic values. Sensitivity to different priors on hyperparameters was also investigated, using flat normal instead of uniforms, with large bounds as in Table 3.

Model selection and posterior checking

The different model formulations were compared using the deviance information criterion (DIC, Spiegelhalter *et al.*, 2002). Internal model consistency was checked using Bayesian posterior checking (Gelman *et al.*, 2004, p. 175), with the procedure described by Michielsens and McAllister (2004). The realized (resp. predicted) discrepancy χ^2_{obs} (resp. χ^2_{pred}) was computed for each stock as a measure of the discrepancy between the observed log(RPSB) (resp. predicted) and the expected log(RPSB) given the posterior parameters. If the model fits appropriately, replicated data should look similar to observations and χ^2_{pred} should not be too different from χ^2_{obs}. The Bayesian p-value is the probability that $\chi^2_{\text{pred}} > \chi^2_{\text{obs}}$ estimated over the posterior sample of the parameters. Very high (e.g. >0.95) or very low (<0.05) p-values provide serious warning (Gelman *et al.*, 2004) about the lack of consistency between the model a posteriori and the data.

Considering observation errors in S *and* R

Recruitment and spawning biomass estimates used in our analysis are derived from stock assessment models; thus, they are surrounded with errors due to the multiple sources of uncertainty in such models. A positive correlation between the errors on S and R could also be expected because of the cohort dynamics in age-structured stock assessment models. Estimates of SR parameters have been shown to be sensitive to observation errors in S and R (Walters and Ludwig, 1981; Walters and Martell, 2004). In particular, considering observation errors affect the balance between the different sources of variability and might in turn affect the estimates of the variance of process errors. To assess how robust our results are to errors in S and R, parameter estimation was also performed by considering that S and R were observed with logNormal errors with expected means centred on S and R values, in addition to the stochasticity in the recruitment process.

Several flatfish stock assessment reports provide the measure of uncertainty in S and R that can be converted in coefficient of variation (CV) of logNormal distributions (Table 2). We rely on those values to fix the variance of observation errors to realistic values and provide a sensitivity analysis of our results to CV ranging from 5 to 30%. Observation errors were included with or without covariance between observation errors on S and R, with a maximum covariance defined as $\sqrt{\mathrm{var}(S)\mathrm{var}(R)}$.

Computational details

Bayesian posterior distributions were approximated via Monte Carlo Markov chain (MCMC) methods using the JAGS software (http://mcmc-jags.sourceforge.net) through the Rjags (www.Rproject.org) package. Three MCMC-independent chains with dispersed initialization points were used. For each chain, the first 5000 iterations were discarded. Inferences were derived from a sample of 3 × 50 000 iterations. All the modelling results have undergone the Gelman–Rubin test (Brooks and Gelman, 1998) as implemented in the R Coda package to assess convergence of MCMC chains (R ratio < 1.05 for all variables).

Assessing the relationship between parameters estimates and life-history traits

Relations between model estimates and different life-history traits of flatfish species were investigated to test for the existence of patterns consistent with the ecological theory. In particular, the following hypotheses were tested: (i) the density-independent component of the variance of the recruitment process (as measured by η_0) is expected to be positively correlated with the duration of the pelagic stages (eggs and larvae), before benthic settlement (Van der Veer *et al.*, 2000); (ii) the intensity of density-dependent regulation (as estimated by β and the heteroscedasticity coefficient η_1) is expected to be positively correlated with the level of dependence to restricted nursery areas (Iles and Beverton, 2000; MacKenzie *et al.*, 2003; Rooper *et al.*, 2004; Craig *et al.*, 2007; Juanes, 2007).

Life-history traits (i.e. the duration of the pelagic stage and the degree of concentration of juveniles in nurseries) were obtained from the literature (Gibson, 2005) for each species (Table 2) as they were not available at the stock level.

Results

Comparison of the recruitment variability across orders

Whatever the model form (Ricker or BH), Pleuronectiforms and Perciforms exhibited lower estimates of recruitment variability than other fish orders (Figure 1). For both BH and Ricker models, p-values of multiple Tukey pairwise comparison tests revealed significant differences between Clupeiforms and Perciforms or Pleuronectiforms and between Gadiforms and Perciforms or Pleuronectiforms. But no significant differences exist between Clupeiforms and Gadiforms or between Perciforms and Pleuronectiforms. Within Pleuronectiforms, the few amount of stocks per species (only one stock for 9 of 17 species) limits the analysis, so no interesting pattern could be found between the residual variance and the species.

HBM for flatfish species

Model selection

Model selection criteria were used to evaluate how well the data support the three nested different modelling assumptions, (i) the average form of the SR model (BH or Ricker), (ii) the existence of heteroscedasticity in the residual variance [$\eta_1 \neq 0$ in Equation (11)], and (iii) the level (species or stocks) at which the variability of η_1 is to be considered.

When S and R are considered known without observation errors, the greatest differences in DIC values were explained by the difference in deviance due to the form of the average SR model, the BH form being systematically selected, with differences in DIC values ≥ 15 in favour of the BH form (Table 4). Within a single form for the average SR model, difference in DIC between models without ($\eta_1 = 0$) or with ($\eta_1 \neq 0$) heteroscedasticity were low. However, the most complex models including heteroscedasticity ($\eta_1 \neq 0$) had always smaller DIC values than the model with constant variance ($\eta_1 = 0$; Table 4). For models including heteroscedasticity, models with η_1 considered variable between stocks (39 parameters) had smaller DIC values than when considering only between species

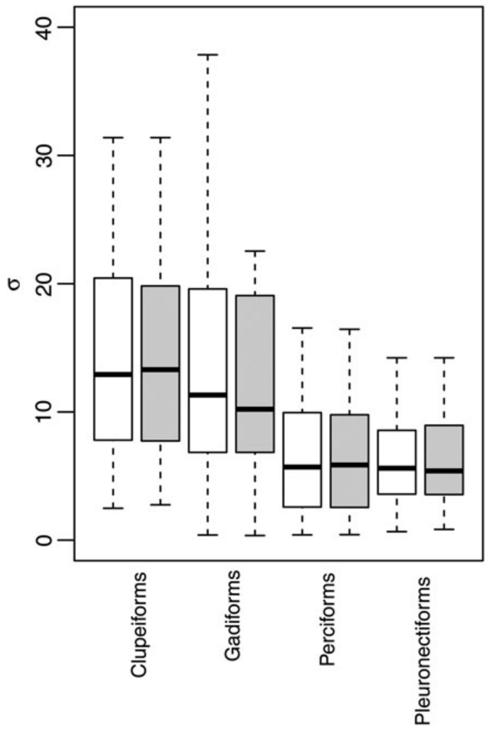

Figure 1. Residual variability around SR models among fish orders. Boxplots represent the between stocks variability of σ estimates (fit by the least-square procedure), obtained under the BH (white) or Ricker models (grey).

Table 4. Differences between the DIC of the BH model with stock-specific η_1 (ref) and other model configurations.

	Beverton–Holt	Ricker
Without observation errors		
$\eta_1 = 0$ (constant variance model)	+3	+21
$\eta_1 \neq 0$ (heteroscedastic variance model)		
Species-specific η_1	+2	+12
Population-specific η_1	ref	+18
With observation errors		
$\eta_1 = 0$ (constant variance model)	+5	+25
$\eta_1 \neq 0$ (heteroscedastic variance model)		
Species-specific η_1	0	+24
Population-specific η_1	ref	+23

Differences are calculated independently for the model without or with observation errors on *S* and *R* (CV = 15%).

variability (17 parameters), but evidence in favour of the most complex model were not so clear. Different types of weakly informative prior distribution affected neither model selection nor parameter estimates and results revealed robust to the existence of observation errors on *S* and *R* (Table 4).

To sum up, even if evidence in favour of a particular model was not very strong, results were in favour of a residual variance that depends on the level of stock ($\eta_1 \neq 0$) for both BH and Ricker forms. Even in the presence of observation errors on *S* and *R*, the BH model form with residual variance depending on the level of stock and with stock-specific η_1 parameters was the best supported by the data. For this model, posterior checking does not reveal any model failure to replicate data comparable with observations. As qualitative results concerning heteroscedasticity are not impacted by the model form (BH vs. Ricker), only the results obtained in the BH model with stock-specific parameter η_1 are detailed in the followings.

Estimates of parameters

Most of the 39 flatfish stocks exhibit a clear decreasing RPSB with increasing stock level (Figure 2). Parameters estimates, as revealed by their marginal posterior distribution in Figure 3, remain largely uncertain as commonly observed when fitting stock–recruit models, especially for the slope at origin α. Some estimations of α are pretty low (e.g. BSAI *R. hippoglossoides*), suggesting poor productivity for some flatfish stocks. Most of the β parameters (back calculated as $\beta = \alpha/K$) are clearly negative, which confirms the decrease in RPSB with the level of stock (Figure 2). However, the joint posterior distribution of (α,*K*) exhibits strong negative correlation, and estimates of α are sensitive to the formulation of the residual variance (negative β induce lower α estimates). There is no clear species pattern for both α and *K* parameters (Figure 3), as the within-species variability is in the same order of magnitude than the across-species variability. This supports the retained exchangeable hierarchical structure on (α/K) across all stocks with no species effect on those parameters.

The residual variance is decreasing with the stock level for almost all the 39 stocks. Indeed, the marginal posterior distributions of parameters η_1 (Figure 4b) have a negative median for almost all stocks (37 of 39) and have more than 75% of their mass in negative values for 29 of the 39 stocks. The posterior distribution of μ_{η_1}, i.e. the grand mean of η_1 across stocks, has its median at −0.40. Estimations of parameters η_0 do not show any particular pattern across species (Figure 4a). As expected because their sum codes for the total residual variance, estimates of parameters η_0 and η_1 for each stock were negatively correlated.

Overall, parameter estimates revealed robust to observation errors on *S* and *R*. Increasing the variance of observation errors logically leads to higher uncertainty on parameter estimates. Estimates of α slightly decrease, whereas those of *K* increase. As shown on Figure 5, estimates of η_1 remain robust for observation errors with CVs of 5 and 15% while they drop for most populations at 30% CV. The introduction of covariance between *S* and *R* observation errors does not strongly affect parameter estimates.

Testing the expected relationships with life-history traits

Data on life-history traits could only be compiled for 10 of the 17 species of Pleuronectiforms. For these ten species, the variability among stocks in estimates of parameters (α, *K*, η_0, η_1) is high and in the same order as interspecific variability (Figures 3 and 4). No pattern can be identified between life-history traits of species (pelagic stage duration, degree of concentration in nurseries) and parameter estimates (e.g. estimates of η_0) do not exhibit any link to larval stage duration (Figure 6), whereas a positive correlation was expected.

Discussion

This analysis offers a substantial contribution to the understanding of the variability of the recruitment process of marine fish, with a particular focus on flatfish species.

A hierarchical meta-analysis of recruitment variability with a focus on flatfish

A theoretical model describing recruitment variability

As a comprehensive model to analyse the recruitment process including concentration at one life stage, we follow Minto *et al.* (2008) to propose a model where recruitment results from the combination of two sequential phases; a first egg/larval pelagic phase with mortality driven by stochastic density-independent processes combined with a second phase where both density-dependent mortality and environmental stochasticity occur. Such a theoretical model revealed a pertinent framework as it allows to formalize that (i) recruitment variability should be lower for species with density-dependence occurring at a later stage in the recruitment process; (ii) for a particular stock, if density-dependence occurs at the latter stage, the recruitment variability should decrease with the level of stock, providing a test for the existence of density-dependence even if noise dominates the signal.

Using stock assessments data to analyse recruitment variability

In his meta-analysis, Minto *et al.* (2008) analysed 147 exploited fish stocks, out of which only seven were flatfish stocks. Iles (1994) explored stock–recruit data for 20 flatfish stocks. Our study used the most up to date stock–recruitment data on exploited flatfish stocks. Thirty-nine flatfish stocks of 17 species were included, and longer time-series were used, thus adding substantive material (+15% of stock × year lines) about suitable flatfish data in the RAM legacy database. As in Minto *et al.* (2008) and Iles (1994) previous works, all stock–recruit series included in our analysis were carefully selected. They were all derived from statistical catch-at-age models (e.g. VPA, XSA, ADAPT) and constitute the best standardized information available. Of course, the quality of the data can be questioned. Stock–recruit estimates from those methods can provide poor estimates for the most recent years but they are more

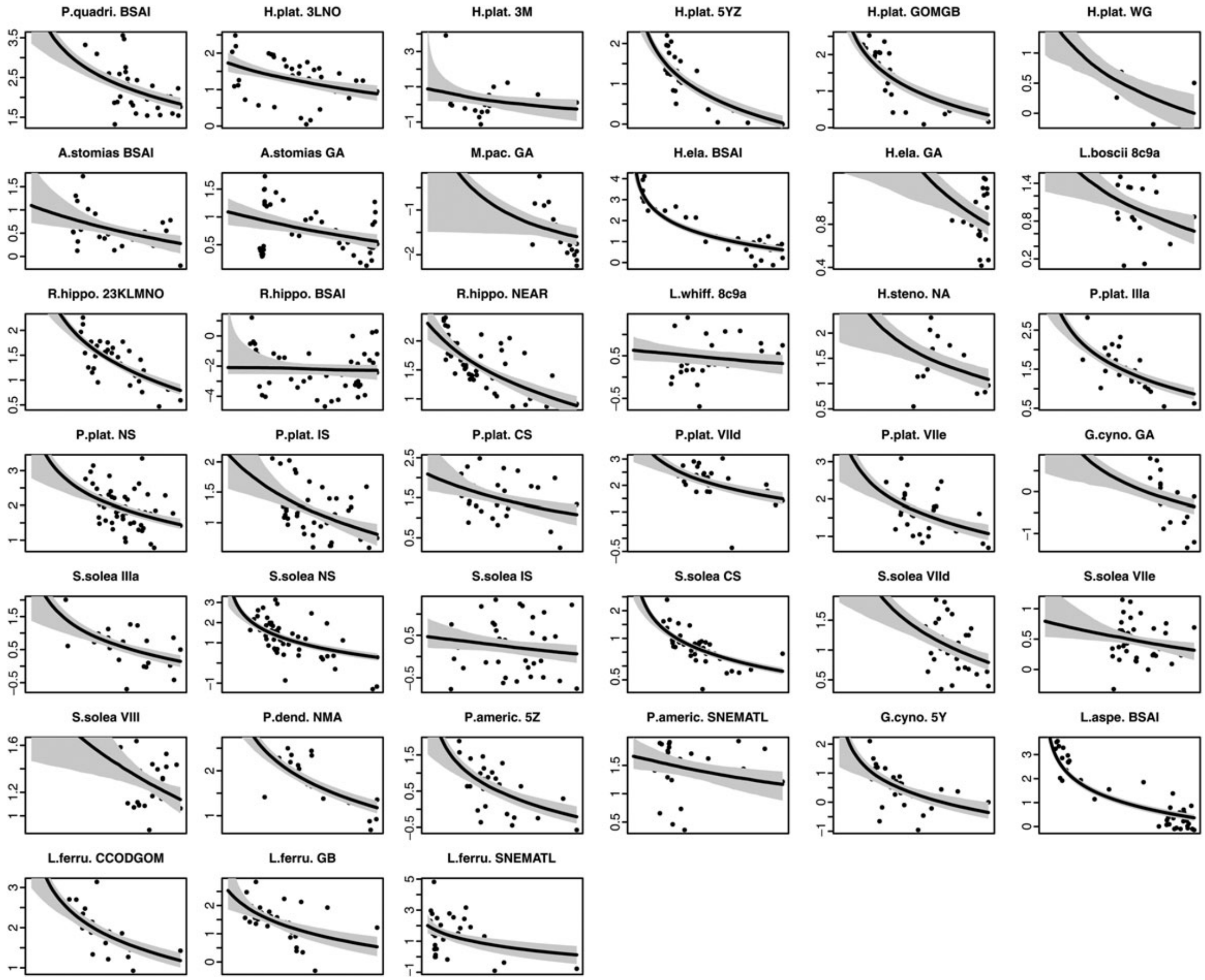

Figure 2. Model fits with 95% Bayesian confidence interval. Model fits are drawn using posterior medians of parameters. Bayesian estimates are obtained under the BH model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific η_1 parameters and no observation errors on *S* and *R*. *x*-axis, values of SSB standardized by max(SSB) (between 0 and 1); *y*-axis, log(RPSB).

standardized than direct estimates from research vessel surveys that can exhibit unduly high variability due to high estimation error. Data standardization can also be the source of additional errors, due for instance to uncertainty in the maximum age that can affect $\mathrm{SPR}_{F=0}$ values used to standardize recruitment series. To account for the existence of errors in *S* and *R* data series, in addition to the recruitment stochasticity, our modelling approach explicitly considers errors caused by mismeasuring *S* and *R* with realistic observation error variance derived from stock-assessment reports. Our results revealed robust to observation errors, strengthening our conclusions.

Testing for signal in recruitment variability

By combining approaches at different scales, including a comparison of the recruitment variability between different fish orders with an analysis of the changes in recruitment variability between low and high levels for 39 flatfish stocks, we provide a body of results consistent with the concentration hypothesis (Iles and Beverton, 2000) for nursery-dependent flatfish species.

Interorder patterns in recruitment variability

Pleuronectiforms exhibit significant lower recruitment variability than most other exploited marine fish species. Most flatfish species go through eggs and larval drift after spawning, inducing density-independent mortality until settlement in suitable nursery habitats (Rochette *et al.*, 2012). As already stated (Bailey, 1994; Van der Veer *et al.*, 2000; Gibson, 2005), because flatfish eggs and larval life stages do not differ from other teleost fish (Gibson, 2005), the variability induced by these stages is likely to be comparable with other teleost fish. The lower recruitment variability observed for flatfish species is then more likely to result from specific processes occurring at a later stage in the recruitment process. This is consistent with the concentration hypothesis (Iles and Beverton, 2000) which suggests that species with juveniles that concentrate in specific nursery habitats should display dampened variations in recruitment, caused by a limited carrying capacity of those nurseries (Le Pape *et al.*, 2003a). Pleuronectiforms are nursery-dependent species (Van der Veer *et al.*, 2000; Gibson, 2005), whose life cycle relies on restricted nursery habitats, compared with a large proportion

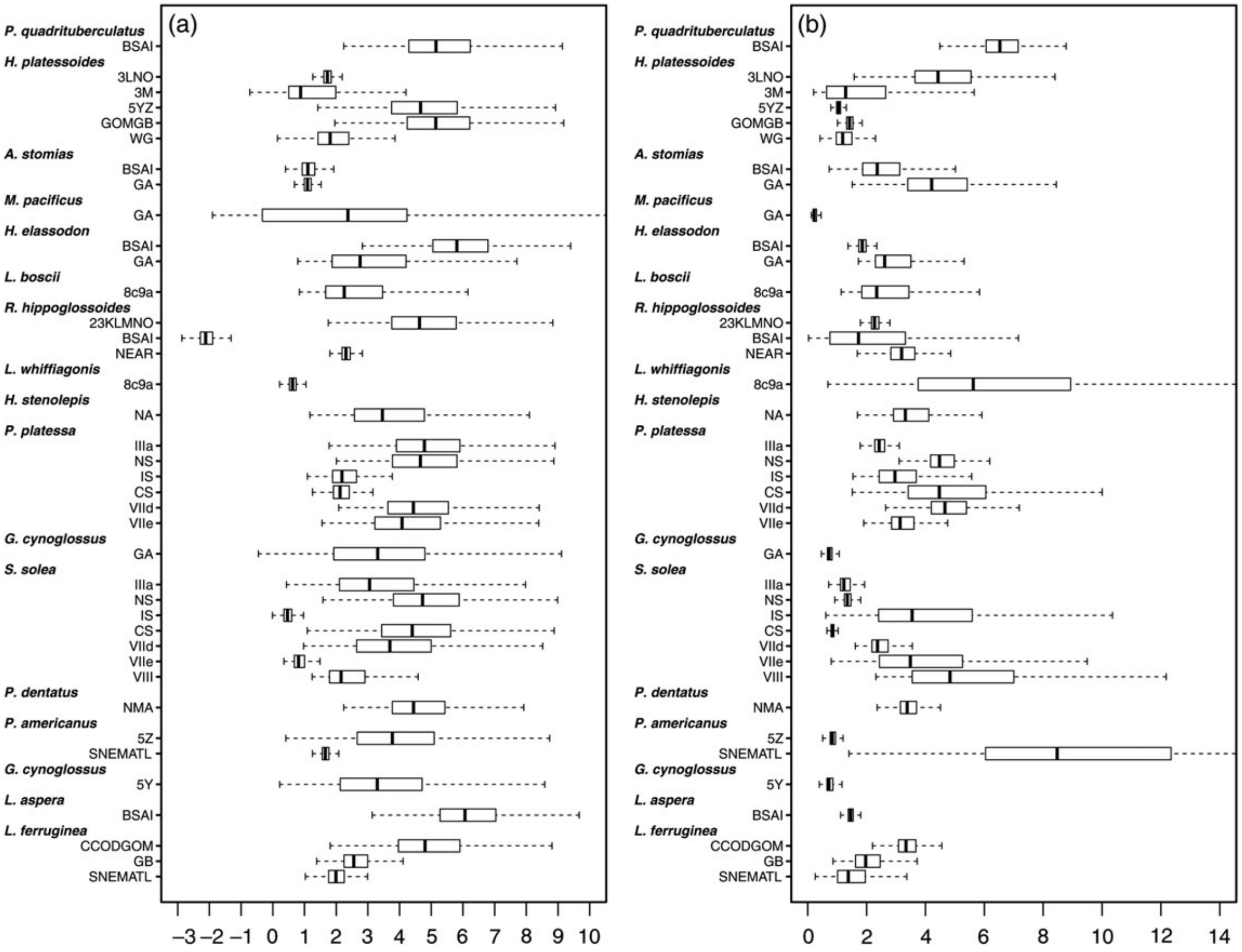

Figure 3. Marginal posterior distributions of parameters α ((a); log scale) and K (b). Bayesian estimates are obtained under the BH model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific η_1 parameters and no observation errors on S and R.

of pelagic (e.g. Clupeiforms) or bentho-demersal (e.g. Gadiforms) species with less restricted juvenile habitats and higher variations in recruitment. More significant differences between orders could even have been expected but a large amount of mechanisms influence survival (Hixon and Jones, 2005; Houde, 2008) leading to important recruitment variability, even for nursery-dependent species as flatfish (Van der Veer *et al.*, 2000).

Stock recruitment relation among flatfish

Stock recruitment models for the 39 flatfish stocks showed a general decreasing RPSB rate when the level of stock increases. SR data generally exhibited highly stochastic recruitment around a rather constant average, even for a relatively wide range of stock levels (Iles, 1994). But when evaluating the RPSB against stock values, this logically leads to a decreasing RPSB with increasing stock level, interpreted as an evidence for a density-dependent relationship between S and R. This was consistent with flatfish literature. Iles (1994) previously explored stock–recruit data for flatfish using the BH, Ricker, and Shepherd generalization forms (Shepherd, 1982). He provided statistical evidence of underlying the stock–recruit relationship for one-third of those stocks, with the model of constant recruitment retained in the two remaining thirds.

Stock recruitment variability among flatfish

Results revealed that the variability of the RPSB decreases when stock size increases, which is consistent with density-dependent processes occurring at a later stage (after the settling phase) after a pelagic drift phase of larvae (Rijnsdorp *et al.*, 1995; van der Veer *et al.*, 2000). The pattern of heteroscedasticity in the variance revealed consistent across almost all flatfish stocks.

Taken individually, each stock provides few information to estimate SR parameters, a fortiori parameters controlling how the variance depends on the stock size. The HBM allowed to borrow strength among the 39 stocks (Rivot and Prévost, 2002; Michielsens and McAllister, 2004; Parent and Rivot, 2012; Pulkkinen and Mäntyniemi, 2013) and provided the estimates of parameters that could not be estimated from single SR datasets (Burrow *et al.*, 2013). Parameters η_0, η_1, and α are independent from the population size by construction, and transferring information between stocks for these parameters is fully justified. Sharing information on K may appear more questionable. However, it is worth noting that because all recruitment data were standardized by the maximum stock size, all K are also standardized by the population size and are in the same order of magnitude. Trials with all K mutually independent between stocks provided similar results as setting a hierarchical structure on K.

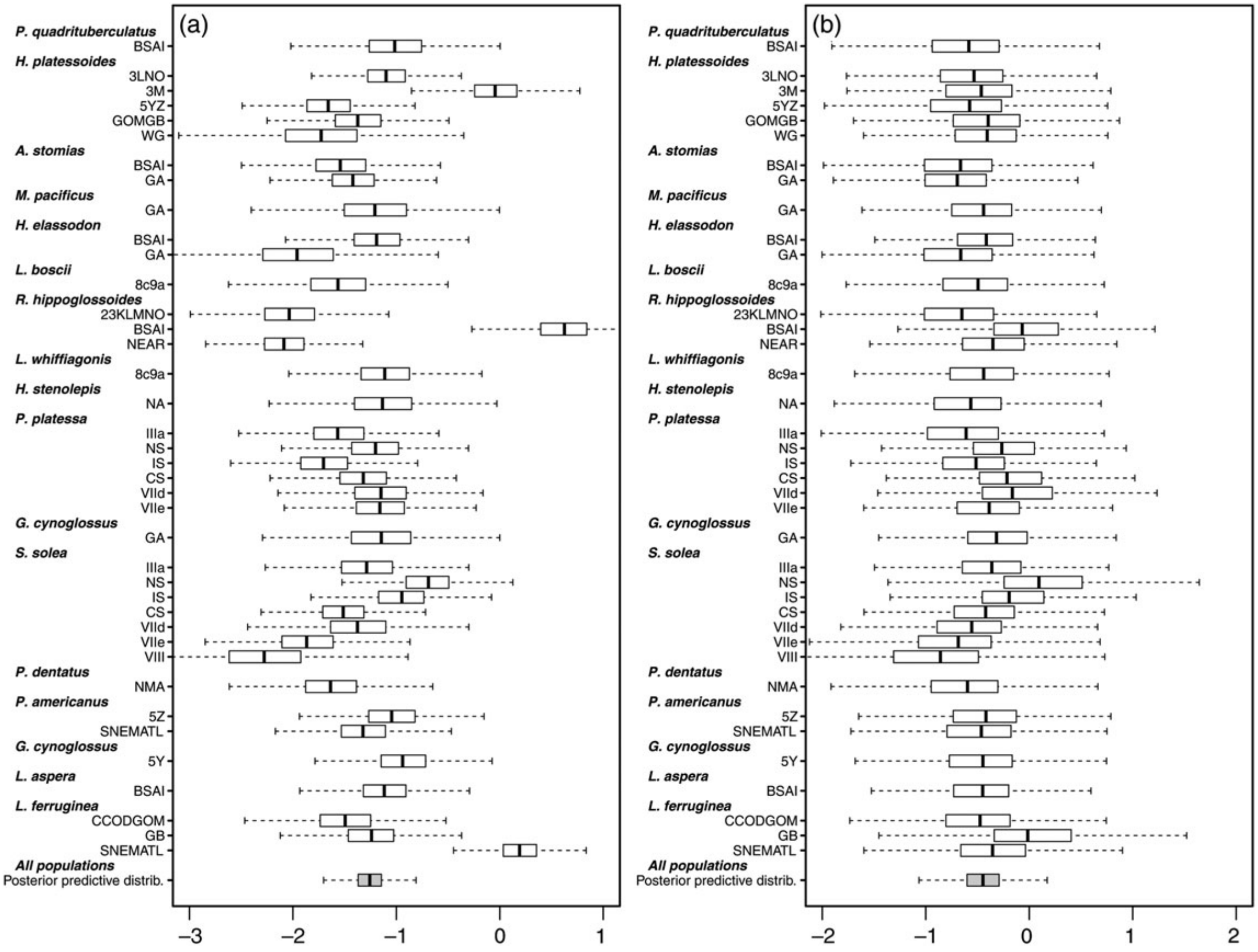

Figure 4. Marginal posterior distributions of parameters η_0 (a) and η_1 (b) for all stocks. Bayesian estimates are obtained under the BH model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific η_1 and no observation errors on *S* and *R*. The posterior predictive distributions (grey boxplots) show the grand mean of parameters estimated across the 39 stocks by the hierarchical model.

Using model selection and validation tools, we were able to compare different model formulations. Results showed that evidence in favour of a model with a decreasing variance with increasing stock size did not depend on the form of the average SR model (Ricker or BH). The model that best support the data was a BH form with all parameters specific to each stock (no generic inter-stocks species effect). As a difference with Minto *et al.* (2008) model in which the heteroscedastic parameter η_1 was estimated at the species level, our results were in favour of stock-specific parameters.

In addition to recruitment stochasticity, we explicitly consider error caused by mismeasuring *S* and *R* (measurement or observation error). Several approaches have been proposed to simultaneously account for process and observation errors in SR analysis. When considering inferences in the maximum likelihood framework, an additional constraint is needed to avoid problem with model identification, and several authors have proposed to fix the proportion of the total variation due to observation errors (Walters and Ludwig, 1981; Schnute, 1994; Schnute and Kronlund, 2002). Because of the influence of priors on all parameters, such constraints can be relaxed in the Bayesian context. Su and Peterman (2012) showed that both process and observation error variances can be estimated simultaneously in SR models considered in a Bayesian state-space framework. Considering the proportion of the total variation due to observation errors as known generally reduces the bias in SR parameter estimates, although the influence of arbitrarily fixing this proportion depends on the productivity parameter (slope at the origin) and the contrast in the levels of stocks. However, fixing the proportion of the total variation due to observation errors was not an appropriate approach for our analysis. Indeed, this would mechanically lead to introduce heteroscedasticity not only in the natural variability but also in the observation errors, and no such a relationship was mentioned in any flatfish stock-assessment report. Following an approach similar to Rivot *et al.* (2001) who used capture-mark-recapture models to provide realistic estimates of observation errors in stock and recruitment, we rely on quantitative estimates of the observation error variance available from stock-assessment reports to fix the CV of observation errors to realistic values. We assess the sensitivity of our results to the value of the CV, with values ranging from CV = 5% to CV = 30%.

Considering observation errors in *S* and *R* does not impact the main conclusions. When the variance of observation errors increases, the proportion of the total variance explained by process errors decreases mechanistically, then estimates of parameters η_1 decreases too. However, even with high level of observation errors, the process error variance significantly increases when

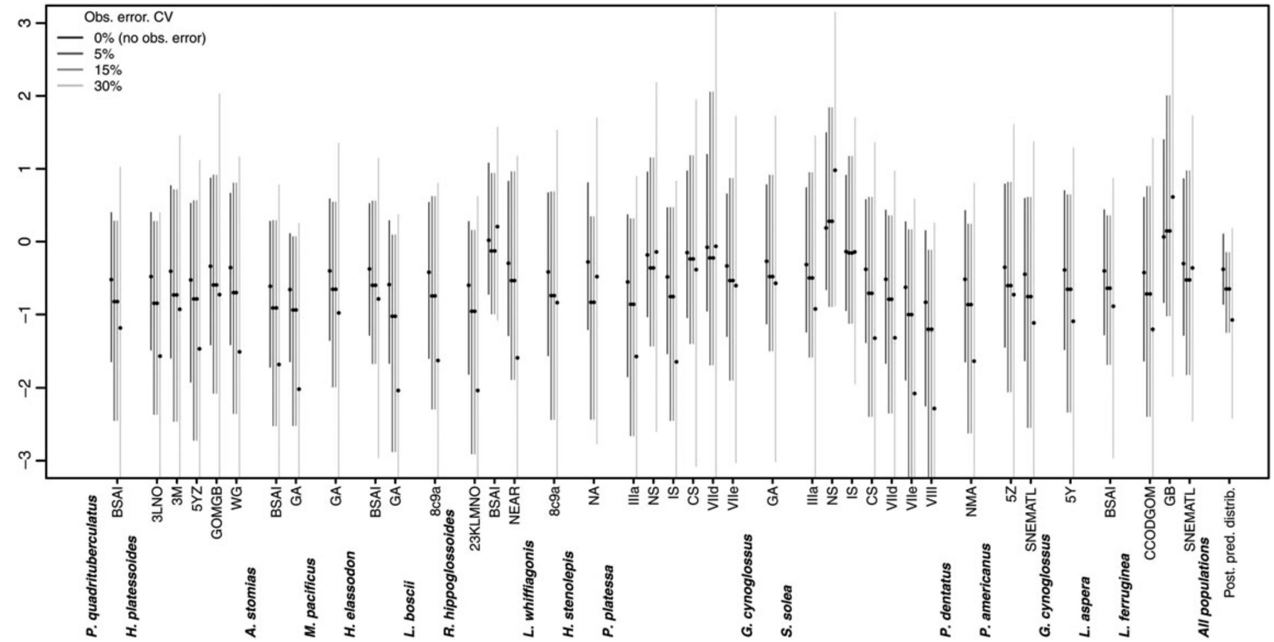

Figure 5. Marginal posterior distributions of η_1 obtained with the BH model with stock-specific η_1 under increasing observation errors levels (CV obs. errors = 0, 5, 15, and 30%; no covariance).

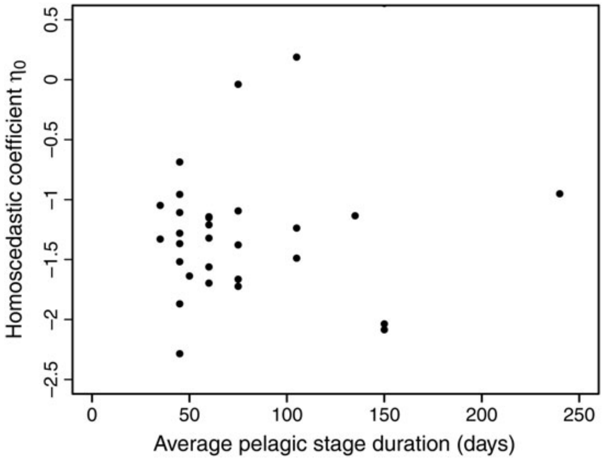

Figure 6. Relation between average pelagic stage duration and posterior estimates (posterior medians) of η_0. Posterior Bayesian estimates are obtained under the BH model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific η_1 parameters.

the level of SSB decreases, indicating that our results are not an artefact due to observation errors in S and R.

But still, our results could have been an artefact due to observation errors on R with a decreasing variance as a function of S. However, would the observation error on R be dependent on the level of S, the variance of observation errors on R would rather be decreasing when S decreases. Indeed flatfish stocks with lower S are generally highly exploited stocks that in turn correspond to more informative catch data and to more precise recruitment estimates.

Habitat dependence at young stages and flatfish stocks management

Our results provide evidence for the existence of density-dependent processes in relation to flatfish nursery habitat, pointing out the dependence of these species to the capacity of their nursery habitat (Rijnsdorp *et al.*, 1992; Rooper *et al.*, 2004). This flags that, for those kind of heavily exploited fish populations, measures aiming at improving or preserving the capacity of juvenile habitat could be especially effective to improve adults' biomass, and even much more effective than regulating fishing effort on the adults (Levin and Stunz, 2005; Van de Wolfshaar *et al.*, 2011).

However, the estimates of the slope at the origin of SR models, α, appeared sensitive to variance formulation, pointing out the sensitivity of estimates of key population dynamic parameters to hypotheses made on the variance, in addition to those made on the average SR models (Burrow *et al.*, 2013; Pulkkinen and Mäntyniemi, 2013). Moreover, it is worth noting that considering heteroscedasticity in the variance may complicate the computation of management reference points such as the MSY (Burrow *et al.*, 2013).

The recruitment variability is stock-specific

One striking result of this study is the absence of species effect in estimates of parameters, as emphasized by the fully exchangeable hierarchical structure between the 39 flatfish stocks. Species effects could be identified in neither the model nor the variance parameters, the within-species variability of parameters being of the same order of magnitude than the between-species variability. As data on life-history traits were only available at the species and not at the stock level, it is not surprising that no relationship between life-history traits and parameter estimates could be found. Indeed, within the Pleuronectiforms order, there are moderate contrasts in life history so interspecific contrasts are limited in the present study. Moreover, intraspecific patterns could be important among stocks belonging to the same species. For instance, larval life history for different stocks may strongly differ for a given species (Rochette *et al.*, 2012). Nursery habitat features may also play a role and the level of density-dependence could vary among stocks for a given species (Le Pape *et al.*, 2003b; Johnson, 2007), with consequences on recruitment variability (Le Pape *et al.*, 2003a). From an evolutionary perspective, life-history traits for a given stock are the consequences of an adaptation to the local conditions encountered (Gibson, 2005; Galland *et al.*, 2013; McBride *et al.*, 2013) preventing the existence of a clear patterns at the species level. Thus, life-history traits depend more on the environment (Félix *et al.*, 2011; Freitas *et al.*, 2012; Comerford *et al.*, 2013; Fincham *et al.*, 2013) than on contrasts among flatfish species. Finally, changes in environmental conditions affecting a given population during the time frame the data were collected are susceptible to occur, either hampering the underlying stock–recruit relationship (Clark and Hare, 2002) or the stability of life traits. As a perspective, it would be of major interest to compare parameter estimations to life-history traits at the stock levels to account for observed differences between stocks and to increase the contrast by extending the analysis to other orders of marine fish.

Acknowledgements

We would also like to thank other people who contributed to complement the database for flatfish stock–recruitment data, especially Tim Loher and Juan Valero from the International Pacific Halibut Commission. We thank the two anonymous reviewers and the associated editor for their useful comments. This work was funded partly by the European Community's Seventh Framework Programme (FP7?2007–2013) under Grant Agreement No. 266445 for the project Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS). This study uses the RAM legacy stock–recruitment database and we would like to thank R. A. Myers and his followers for rending these data available.

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Handling editor: Shijie Zhou

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2141–2151. doi:10.1093/icesjms/fsu035

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

The dynamics of fish populations at low abundance and prospects for rebuilding and recovery

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Hilborn, R., Hively, D. J., Jensen, O. P., and Branch, T. A. The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. – ICES Journal of Marine Science, 71: 2141–2151.

Received 19 July 2013; accepted 13 February 2014; advance access publication 30 March 2014.

Previous meta-analysis of spawner–recruit relationships suggested that depensatory behaviour is uncommon, and stocks pushed to low abundance are unlikely to suffer decreases in recruitment more severe than would be expected based on the decline in spawning stock. Using an updated database that has over 100 stocks that were depleted to less than 20% of their maximum observed stock size, we tested for depensatory behaviour in both total surplus production and recruitment and we also examined the probability of stock increase as a function of stock size and fishing pressure. The number of stocks that showed a significant improvement with depensatory models was less than that expected by chance. Hierarchical meta-analysis showed that the majority of the evidence was for no depensatory behaviour but could not rule out depensation at very low stock sizes. Stocks that are depleted to low abundance are expected to rebuild when fishing pressure is reduced if the environment has not changed but there is considerable evidence that the majority of fish stocks are impacted by changes in productivity regimes. Nevertheless, if stocks are very heavily depleted and fishing pressure is not reduced to quite low levels, the expected recovery time is both uncertain and long. Very low abundance should clearly be avoided for many reasons and the range of abundance where depensation cannot be ruled out is well below commonly adopted limit reference points.

Keywords: depensation, low density dynamic, rebuilding, recovery, regime changes.

Introduction

It is 100 years since the publication of Johan Hjort's classic work "Fluctuations in the great fisheries of northern Europe viewed in the light of biological research" (Hjort, 1914). In this monograph, Hjort considered what was known at the time about the causes of fluctuations in fish stocks and specifically addressed what was known about the formation of year-class strengths in relation to spawning stock abundance. Hjort found little relation between the two and stated "A rich spawning may produce a year class poor in numbers, while a large year class may have its origin in a year when the spawning was at its lowest." In the last 100 years, we have acquired considerably more information about the behaviour of populations at low abundance and are able to expand considerably upon Hjort's understanding.

Perhaps, the most influential fisheries event in the last 50 years was the collapse and closure of the northern cod fishery in Eastern Canada in the early 1990s (Hutchings and Myers, 1994; Rice, 2006). Tens of thousands of people were put out of work, and the developing system of fisheries assessment and science was brought into question. A key issue raised by the cod collapse is the dynamics of stocks at low densities, and the potential for multiple stable states, where once pushed to a low abundance, populations might be stuck in that condition despite reduced fishing pressure. Walters and Kitchell (2001) used trophic models to show how such multiple stable states could arise, and Worm and Myers (2003) documented many cases of where the depletion of demersal fish species led to ecosystem changes often characterized by increases in invertebrate abundance. Others have shown that ecosystem state changes associated with fishing on other parts of the ecosystem (Anderson and Piatt, 1999; Utne-Palm *et al.*, 2010).

The 1990s saw a renewed interest in the relationship between spawning stock and abundance, and Myers *et al.* (1994) used a compilation of over 100 spawner–recruit relationships to argue that there was good evidence that lower spawning stocks produced lower average recruitments. At about the same time, there was work on whether rates of increase declined at low densities (known as depensation), a necessary condition for multiple stable states, and Myers *et al.* (1995) and Liermann and Hilborn (1997) found little evidence of depensation. Liermann and Hilborn (1997) state "we . . . found that, for all of the taxa, the most likely values fell close to or within the range of no depensation". Using the same database as Myers *et al.* (1994), these two papers showed that per capita recruitment rates continually increased as the density of spawning stock was reduced.

The dynamics of populations at low densities play a crucial role in understanding extinction processes, as well as in the long-term dynamics of populations and ecosystems (Dulvy *et al.*, 2003; Reynolds *et al.*, 2005). Density-dependent rates of increase can be classified into two types, compensatory rates in which the per capita growth rate of a population increases as density decreases and depensatory rates where the per capita growth rate decreases as density decreases. Common mechanisms that lead to compensation include more food per individual at low densities, each individual more likely to find refuge habitat from predators at low densities and lower disease transmission rates at low densities. Compensatory rates lead to population stability, although very strong compensation, when combined with discrete time dynamics, can produce chaotic behaviour (May, 1976). Compensatory rates of increase have been identified in a wide range of species and indeed almost all discussion of density-dependence assumes compensatory processes.

Depensatory processes can include predation if the number killed by predators is largely independent of the abundance of the population (Roemer *et al.*, 2002), group facilitation where at low densities such mechanisms as predator detection are less effective, habitat conditioning where individuals improve habitat quality for others, or the reduced probability of finding mates at low densities (often called the Allee effect; Liermann and Hilborn, 2001). Depensatory processes can lead to much more complex dynamics and have been the object of considerable speculation and exploration within the theoretical literature (Courchamp *et al.*, 1999; Stephens and Sutherland, 1999). Multiple stable states generally require the population rate of increase to go negative at low densities, a condition known as "critical" depensation.

Both the studies of depensation (Myers *et al.*, 1995; Liermann and Hilborn, 1997) used a dataset that contained estimates of the population size and the subsequent recruitment for hundreds of fish stocks. Myers *et al.* tested for the presence of depensation using a tradition *p*-value hypothesis test, comparing a model with and without depensation. They found little evidence for depensation, with no more stocks showing significance than would be expected by chance and concluded that "depensatory dynamics are not apparent for fish populations at the levels studied". Liermann and Hilborn used a Bayesian approach to calculate the intensity of depensatory processes and for the dataset as a whole found little support for depensatory processes.

A major limitation of the data used in both studies was the few number of populations that were observed at low abundance. Of the 128 datasets examined, only 26 had high statistical power. The dataset used in these two studies has recently been updated to include 15 more years of data for fish stocks that were often driven to low densities (Ricard *et al.*, 2012), thus providing a more powerful dataset to determining the frequency and intensity of depensation. In the intervening 17 years since the publication of the first paper, much more attention has been directed towards concerns about fish stock abundance and the impact of fishing on individual stocks and marine ecosystems.

The collapse of eastern Canadian cod (and other groundfish) also led to a focus on the frequency and intensity of fish stock collapses. Meta-analysis of changes in stock abundance showed that large declines in fish stock abundance were quite common and that some taxa (particularly clupeids) recovered about as frequently as they declined (Hilborn, 1997; Hutchings, 2000). Other taxa (especially gadids) showed much less frequent recovery. Hutchings and Reynolds (2004) argued that "reductions in fishing pressure, although clearly necessary for population recovery, are often insufficient" and heightened concern that populations pushed to low densities may not recover even when fishing pressure is reduced. More recent papers (Hutchings *et al.*, 2012a, b) have explored life history correlates with extinction risk and recovery failure.

Mace (2004) criticized Hutchings' (2000) conclusions, pointing out that he had not taken into account whether the fishing pressure had been reduced enough to expect recovery and that the dataseries terminated in the early 1990s which did not allow enough time to see if recovery would actually take place if fishing pressure were sufficiently reduced.

Using an updated version of Myers' 1990s database (Ricard *et al.*, 2012) that generally extends time-series at least 10 years beyond those in Myers' database, a number of results have emerged that provide a much better understanding of the dynamics of fish stocks. Between the early 1990s and the mid to late 2000s, we saw many stocks pushed to low abundance and many stocks recover from overfishing.

Keith and Hutchings (2012) used a non-parametric model to explore evidence for depensatory and compensatory dynamics in spawner–recruit data using the updated dataset and largely confirmed the earlier analysis. "…there is strong evidence of an Allee effect for only 1 of 104 species at their lowest recorded SSB … there is weak evidence of an Allee effect in another three species."

Neubauer *et al.* (2013) used the updated database and found that stocks did indeed recover if fishing pressure was reduced and that once the exploitation rate was reduced to the level that would produce long-term maximum sustainable yield (often called FMSY), recovery was generally expected within 20 years, although populations with unusually low intrinsic rates of increase or those depleted to very low levels are expected to take longer (Figure 3B of their paper). This is a considerably different conclusion than the earlier work by Hutchings and Reynolds (2004). Stochastic changes in productivity also appear to play a large role in the recovery process. The chance of recovery to B_{MSY} within 10 years for a mildly depleted stock (40% of B_{MSY}) is nearly 50% even at fishing mortality rates up to 1.5 times F_{MSY} (Figure 2D of their paper), though of course a stock fished at this rate would not be predicted to remain above B_{MSY} for long.

The conclusion of Myers *et al.* (1994) that low spawning stock led to low recruitment was challenged by Gilbert (1997), who argued that recruitment in marine fish stocks is largely driven by environmental conditions that come in regimes of good and bad. Gilbert suggested that when environmental conditions move from good to bad, recruitment declines, and as a result spawning stock declines, thus giving the impression that lower spawning stocks lead to lower recruitment, when the causal mechanism is instead that lower recruitment leads to lower spawning stocks. When environment changes from bad to good, recruitment increases, spawning stock increases, and again it looks like larger spawning stocks lead to more recruitment.

Vert-pre *et al.* (2013) and Vert-pre (2013) explored the Gilbert hypothesis by examining whether changes in recruitment and surplus production were more tightly linked to biomass changes or shifting environmental regimes. They defined regimes as discrete changes in average surplus production or recruitment. For both measures of stock productivity, they found far more evidence that productivity changes are driven by periodic environmental shifts than by changes in adult biomass. For only 15% of stocks were changes in recruitment best explained by changes in biomass and for 24% of stocks changes in surplus production were best explained by changes in biomass. Table 1 summarizes these results with respect to four hypotheses—that recruitment or surplus production is driven by environmental regimes, that it is driven by stock biomass, that it is a result of a mix of environmental regimes and biomass, or that it is totally random.

Although the mixed model does include an effect of stock biomass, they found that 80% of the variability in surplus production in the mixed-model cases was due to changes in regime, and only 20% from changes in biomass. Their results provide strong evidence that biomass only weakly affects the recruitment or production and that the assumption that stock productivity or recruitment will rebuild by increasing stock size is poorly supported.

Furthermore, the changes in productivity are quite large. Figure 1 shows the frequency of regime changes, scaled so that +1 represents cases where the productivity increased by the mean productivity value over the time-series and −1 represent cases where productivity decreased by the mean productivity.

In this paper, we recast the question of low density dynamics in several ways. First, we formulate a depensation model that can be used for hierarchic meta-analysis and is derived from first principles. Second, we extend this approach from stock–recruitment (the focus of the work by Myers *et al.*, 1995 and Liermann and Hilborn, 1997) to surplus production. This extension recognizes the possibility that depensatory processes may operate not only through changes in juvenile survival (i.e. through the stock–recruitment relationship), but also through other vital rates which contribute to population growth, including adult survival and somatic growth. Both models are applied to data from the updated RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012). Finally, we explore the empirical relationship between stock size, fishing pressure, and probability of stock size increasing.

Material and methods

Models of depensatory recruitment

Previous models of depensation used by Myers *et al.* (1995) and Liermann and Hilborn (1997) used *ad hoc* models that modified compensatory models to reduce the rate of increase at lower densities. We derived a model based on first principles, using the Allee effect as an example of a depensatory process, but we believe that this formulation can capture a range of possible processes. In the Allee effect, the probability of being mated or eggs being fertilized declines at low abundance because at low abundance females may not encounter a male. We assume that contact between individuals of the two sexes is a random encounter process, with the probability of any individual female encountering any individual male being p. If N is the number of males in the population then the probability that an individual female will encounter no males and thus not be mated is the product of a Bernoulli trial with each male and this will in turn be approximately Poisson-distributed. Thus, the probably of not being mated can be assumed to be the zero class of this Poisson distribution [Equation (1)].

Table 1. The proportion of fish stocks for which different mechanisms best explain recruitment and surplus production from Vert-pre *et al.* (2013) and Vert-pre (2013).

Causal mechanism	Recruitment (%)	Surplus production (%)
Environmental regimes	50	27
Stock biomass	15	24
A mixed hypothesis	17	45
Random	18	4

$$\begin{aligned}\Pr(\text{no mating}) &= \frac{\exp(-pN)(pN)^0}{0!}\\ &= \frac{\exp(-pN)1}{1} = \exp(-pN).\end{aligned} \tag{1}$$

The probability of being mated is simply 1 minus the probability of not being mated [Equation (2)].

$$\Pr(\text{being mated}) = 1 - \exp(-pN) \tag{2}$$

This function is parameterized to define the depensation parameter as the population size at which 50% of the population is mated, N_{50}, which is used to produce the depensation parameter q that measures N_{50} relative to the maximum population size [Equation (3)].

$$\begin{aligned}0.5 = 1 - \exp(-pN_{50}) \rightarrow p &= -\frac{\log(0.5)}{N_{50}}\\ \Pr(\text{being mated}) &= 1 - \exp\left(\log(0.5)\frac{N}{N_{50}}\right)\\ &= 1 - \exp\left(\frac{\log(0.5)N}{q\max(N)}\right).\end{aligned} \tag{3}$$

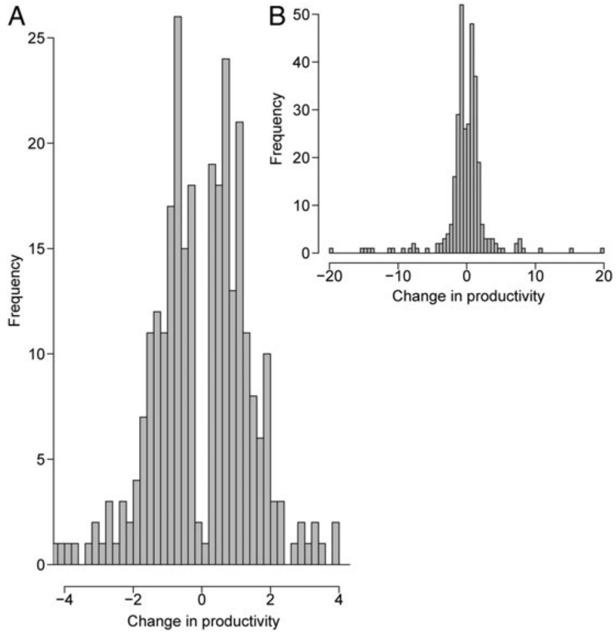

Figure 1. Frequency of productivity changes from either regime or mixed models. The gap around zero on the *x*-axis occurs because the algorithm to detect regime changes does not identify small changes. From Vert-pre *et al.* (2013).

The choice of 50% is totally arbitrary and has no impact on the interpretation of the analysis. If we had chosen 20% then the posterior distributions would have shifted farther to the right, but when actually applied in a model the choice of N_{50} could have been replaced with any other level with no difference in conclusions about the intensity of depensation.

In most marine fish stocks, the parental stock in spawner–recruit analysis is normally referred to as the spawning-stock biomass (B_t), calculated as the number of individuals at age times the weight of females at age, and is often adjusted by the maturity-at-age. We thus define a depensatory impact that reflects the fraction of females who are mated [Equation (4)]. Although it would be better to use a biomass reference point such as the unfished equilibrium spawning population instead of the largest observed stock size, this reference point is often not available or very poorly estimated.

$$D_t = 1 - \exp\left(\frac{\log(0.5)B_t}{q\max(B)}\right) \tag{4}$$

Although this formulation of depensation is derived from the Allee effect and finding mates, it captures a range of depensatory processes with a single parameter q that has a straightforward biological interpretation and is amenable to hierarchical meta-analysis. Scaling depensation to the maximum observed biomass is done to scale N_{50} relative to the scale of the population (which may run from tens of tonnes to hundreds of thousands).

The relationship between the spawning biomass of the stock and the subsequent production of offspring, known as the stock–recruitment relationship in fisheries, has commonly used one of the two models. The Beverton–Holt model is derived from the assumption that compensatory processes from birth until measured as recruitment (often 1 year) is continuous. That is, the instantaneous rate of survival of a cohort depends linearly on its densities. The Ricker model assumes, instead, that the rate of survival depends on the initial cohort size. The derivation of both models is shown in Hilborn and Walters (1992), and Walters and Korman (1999) demonstrate that the Beverton–Holt model follows directly from arena foraging theory that evaluates foraging strategies in light of predation risk. Although the best fit for these two models for many datasets is often quite similar, there are consequential differences for population dynamics and management reference points such as maximum sustainable yield.

A more general model is the Deriso stock–recruitment function [Equation (5)], introduced in Deriso (1980), where B_t is the biomass at time t and R_t is the number of recruits generated from B_t. The Deriso model has a flexible range of shapes and is able to recreate the Beverton-Holt curve with $g = 1$ and the Ricker curve with $g \to \infty$.

$$R_t = \frac{aB_t}{(1 + bB_t)^g}\exp(\varepsilon_t) \tag{5}$$

To include a depensatory model with the Deriso model, we multiply the biomass terms in the Deriso curve by the depensation process [Equation (4)] to obtain the depensatory stock recruitment curve shown in Equation (6). The depensation parameter q is bounded between (0,1), and $q \approx 0$ indicates no depensatory dynamics since recruitment simplifies to the Deriso model.

$$\begin{aligned} R_t &= \frac{aB_tD_t}{(1 + bB_tD_t)^g}\exp(\varepsilon_t) \\ D_t &= 1 - \exp\left(\frac{\log(0.5)B_t}{q \quad \max(B)}\right). \end{aligned} \tag{6}$$

We estimated the parameters of the Deriso model with and without the depensation function and compared model estimates of recruitment with the observed recruitment using AICc. We used a log-normal likelihood function

$$\begin{aligned} L(a, b, g; R, B) &= \prod_t \frac{1}{R_t\sqrt{2\pi\sigma^2}} \\ &\exp\left(-\frac{1}{2\sigma^2}\left(\log(R_t) - \log\left(\frac{aB_tD_t}{(1 + bB_tD_t)^g}\right)\right)\right). \end{aligned} \tag{7}$$

Because the depensation function [Equation (4)] is new, we also did the same analysis using the depensatory function used by Myers *et al.* (1995) shown in Equation (8).

$$R_t = \frac{a{B_t}^{\delta}}{1 + b{B_t}^{\delta}}. \tag{8}$$

In this equation, δ is the depensation parameter, and when $\delta > 1$ the population exhibits depensation. The parameters a and b are the same as those in the Deriso model when $g = 1$.

Models of depensatory surplus production

Surplus production is the change in biomass that would occur in the absence of harvesting and results from the combined effects of recruitment, somatic growth, and natural mortality. A number of papers have explored surplus production patterns in fish stocks (Hilborn, 2001; Jacobson *et al.*, 2001; Walters *et al.*, 2008).

Surplus production is defined as the net change in biomass, plus harvest.

$$S_t = B_{t+1} - B_t + C_t. \tag{9}$$

Where S_t is the surplus production over year t, B_t the stock total biomass at time t, and C_t the catch removed between times t and $t + 1$.

A Pella–Tomlinson surplus production model (Pella and Tomlinson, 1969) was fitted to the data with and without depensation. The Pella–Tomlinson model was chosen rather than the more well-known Schaefer (logistic) model to allow more flexibility in the shape of the production function and because a recent meta-analysis has determined that the shape of the productivity vs. biomass relationship is variable (Thorson *et al.*, 2012). The Pella–Tomlinson model can be written as:

$$\begin{aligned} S_t &= \gamma m\left(\frac{B_t}{B_\infty}\right) - \gamma m\left(\frac{B_t}{B_\infty}\right)^n \\ \gamma &= \frac{n^{n/n-1}}{n-1} \end{aligned}. \tag{10}$$

Where S_t is the predicted surplus production over year t, B_∞ the carrying capacity, m the maximum sustainable yield, and n a parameter that determines the shape of the production function. To add depensation, we multiplied the predicted surplus production times the depensatory Equation (4). Because surplus production can take on both positive and negative values, we used a normal likelihood.

Hierarchical Bayesian analysis of depensation

We treated the depensation parameter for each stock s, q_s, as random variables distributed about a population mean and conducted a Bayesian analysis which provides the posterior predictive distribution of q for any new stock s that can be used as a prior distribution.

Using the Deriso model with depensation from Equation (6), we have parameters a, b, g, q, and σ for each individual stock. The key to the hierarchical model formulation for the depensation parameter q_i for any stock is that we assume that it is drawn from a beta distribution that has a two parameters α and β.

The recruits in year t for stock s are given by

$$\begin{aligned} R_{ts} &= \frac{a_s B_{ts} D_{ts}}{(1 + b_s B_{ts} D_{ts})^g} \exp(\varepsilon_{ts}) \\ D_{ts} &= 1 - \exp\left(\frac{\log(0.5) B_{ts}}{q_s \quad \max(B_s)}\right), \end{aligned} \tag{11}$$

where for each stock s, the ε_{ts} are independently and identically normally distributed with a zero mean and a variance σ_s^2.

$$q_i \sim Beta\,(\alpha, \beta). \tag{12}$$

The parameters a_s, b_s, g_s σ_s, α, and β were assumed to be uniformly distributed with a broad uniform prior (Table 2). The posterior distributions on all the parameters were found using JAGS software, with 100 000 MCMC runs. We used the following diagnostics: the Geweke diagnostic, which compares the first 10% and last 50% of the Markov chain to see if they come from the same distribution; the Raftery and Lewis diagnostic, which calculates the number of iterations and burn-in necessary to generate accurate results with 95% probability; the Heidelberg and Welch diagnostic, which tests the null hypothesis of the Markov chain being from a stationary distribution. We also examined the Gelman–Rubin diagnostic and it indicated no problems with convergence. Autocorrelation and trace plots (for mixing) were also evaluated.

We conducted the Bayesian analysis separately for four taxonomic groups, invertebrates, pelagics, sharks, rays, and skates, and demersal species. For the recruitment analysis, the number of stocks in each group was 5, 33, 2, and 73, respectively. For the surplus production analysis, the number of stocks was 16, 28, 1, and 66.

Data

The data are gathered from the RAM Legacy Stock Assessment Database version 1.0 (Ricard *et al.*, 2012). Only stocks with time-series for biomass (either total biomass above a specific age as presented in the assessment or spawning-stock biomass) and recruits are included in the analysis. For the spawner–recruit analysis, we are using total biomass as a surrogate for spawning stock when spawning stock size was not available. For the surplus production analysis, one could argue that total biomass would be more appropriate, since somatic growth and natural mortality affect total biomass. Stocks are also excluded which include data that clearly exhibit that the recruitment or surplus production were deterministic model output. Deterministic model output was indicated if either the surplus production or recruitment followed a smooth curve when plotted against biomass. For each stock, years are only included if present in both the biomass and recruits time-series. This results in data compiled from 242 stocks. Of these 242 stocks, we eliminated any stocks that were not observed to have fallen below 20% of maximum observed biomass, leaving 111 stocks for surplus production analysis and 113 stocks for spawner recruit analysis.

Table 2. Priors used for Bayesian analysis of spawner–recruit data.

Parameter	Prior
a_s	Uniform 0–10 times the max$R$/max$B$
b_s	Uniform 0–10 times max (R)
G_s	Uniform 0–100
σ_s	Uniform 0–5
α	Uniform 0–10
β	Uniform 0–100

Empirical rates of change

The key question is how likely are stocks to rebuild as a function of the stock abundance and the exploitation rate. The logistic growth model is the simplest formulation of population dynamics that addresses this, and the well-known result (Hilborn and Walters, 1992) is that if we plot the rate of increase with biomass on the x-axis and the exploitation rate on the y-axis, there is an isocline going from (0,r/2) to (k/2,0) that represents the division between the parameter space where the stock increases (below and to the left of this line) and the region where stock size decreases (above and to the right). The axis can be transformed into dimensions B/BMSY and U/UMSY in what is now commonly referred to as a Kobe plot (Worm *et al.*, 2009, Figure 3b).

In the RAM Legacy database, we currently have 358 stocks with estimates of B/BMSY and U/UMSY. For each year for each stock, we can locate it in the space B/BMSY and U/UMSY and determine the direction change. We calculate the proportion of stocks that increased when in that region of B/BMSY and U/UMSY space and plot these probabilities. If stocks show strictly compensatory rates of change then we would expect that stocks would be as likely to increase as decrease around the isoclines connecting (0,UMSY) and (BMSY,0) and be more likely to increase the more the stock was in the lower left hand corner, and more likely to decrease towards the upper right hand corner. If depensation was present then the probability of increase would decline as biomass decreased.

Results

Depensation in stock and recruitment

Maximum likelihood

Of the 113 stocks we analysed, only 4 showed an improved AICc when depensation was added to the Deriso model. The Myers model also showed only four stocks had AICc improvements and an estimated value of δ that is greater than 1. The Deriso model provides quite a bit more flexibility in fitting the data, especially allowing for declining right hand limbs, and this flexibility appears to facilitate improvements in fit when adding the depensation term. Figure 2 shows the fitted spawner recruit data for the Deriso model for the four stocks that showed AICc improvement. Values of the estimated depensation parameter q for these stocks were 0.04, 0.06, 0.30, and 0.97 with AICc improvements of 5.4, 1.7, 0.68, and 0.08, respectively. The stock with an estimated of $q = 0.97$ had very broad confidence intervals.

The three stocks the Myers model in our analysis identified as having significantly improved AICc by adding depensation were

North Sea Herring, Greenland Halibut 23KLMNO and NAFO Cod 3NO. The North Sea Herring and NAFO Cod 3NO were identified as the first and third biggest improvement in AICc using the Deriso model, but the Greenland Halibut 23KLMNO, did not show a significant depensation effect with the Deriso model. The Deriso model without depensation fits the data for this stock much better because it has a declining right hand limb that the Myers model cannot capture.

Bayesian analysis

The Bayesian analysis also showed little evidence for depensation. The posterior predictive distributions of the depensation parameter (in essence the prior for q for a stock with no data) are shown in Figure 3 for the Deriso model. For all four taxa, the mode is near zero, and for pelagic and demersal with good sample sizes, there is almost no weight for $q > 0.04$. For invertebrates with a much smaller sample size, there is some density out to 0.10, and for sharks, rays, and skates with only two stocks, really no inference about depensation can be made. For invertebrates, higher qs are less likely but the data are not particularly informative. These results overall reflects the fact that there is little evidence for depensatory dynamics, but because so few stocks have been to very low stock size, there is not enough data to rule out depensation at very low stock sizes. The high values of q estimated for some of the stocks in the maximum likelihood analysis have almost no weight in the Bayesian analysis, because the data for these stocks can be

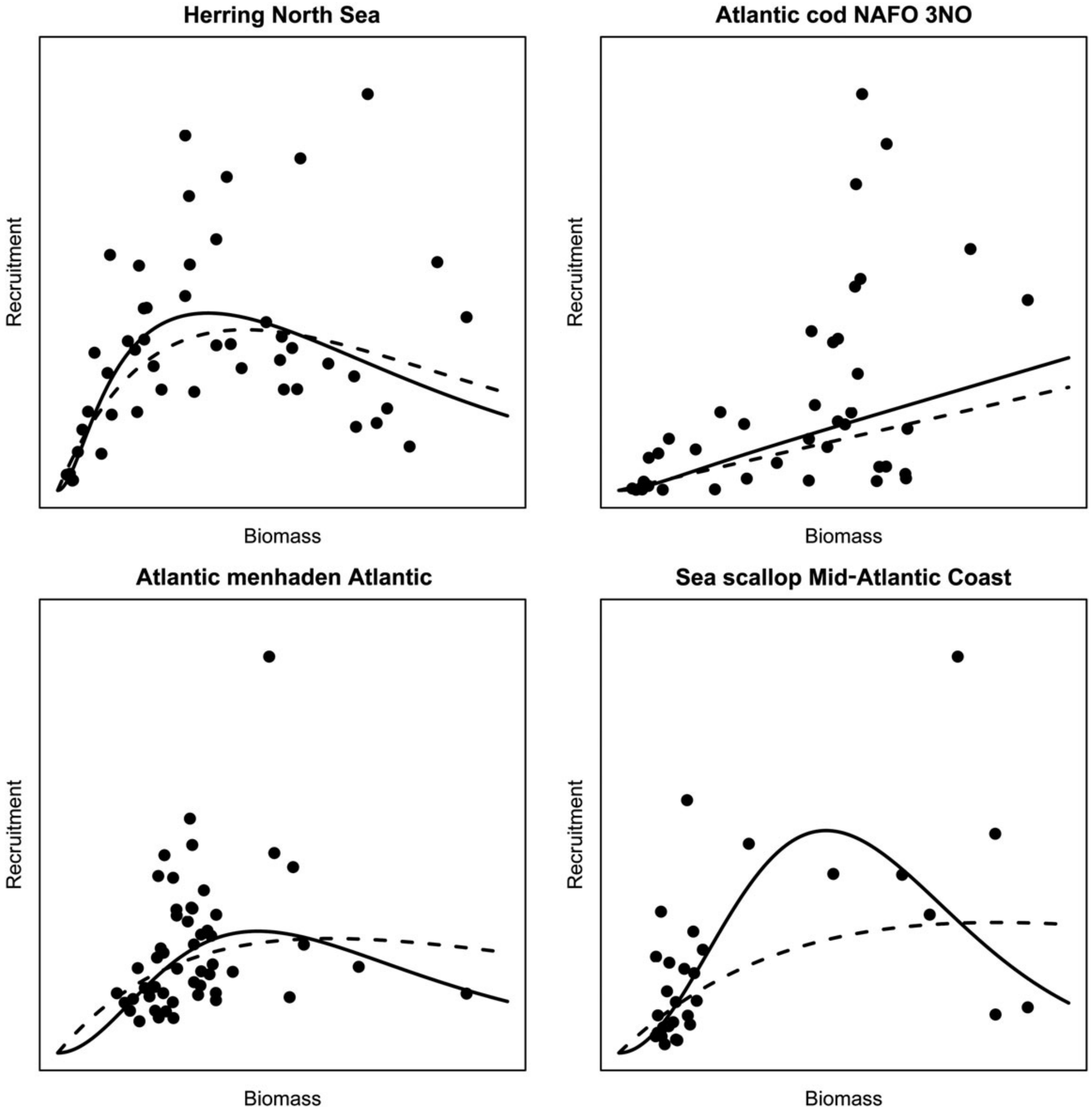

Figure 2. Stock – recruitment data and fits with and without depensation for the four stocks with improved AICc scores for the depensatory model. x-axis is spawning stock and y-axis recruitment. The dashed line is the model fit without depensation and the solid line with depensation.

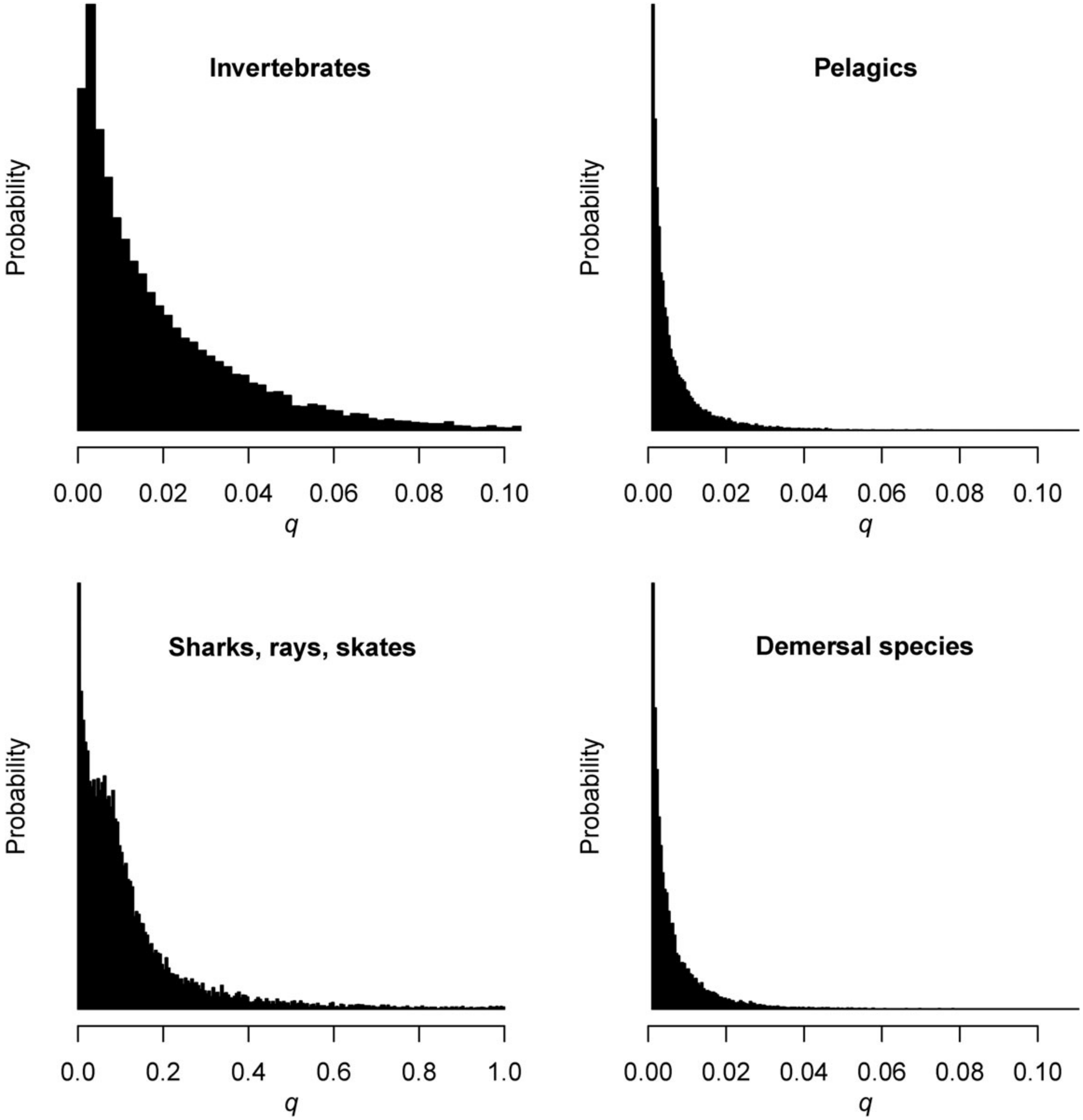

Figure 3. Posterior predictive distribution of the depensation parameter for the Deriso spawner–recruit model for four taxa.

fit almost equally well with very low values of q (the best AICc improvements was 0.08) and many stocks with low q make these low q values much more probable.

Depensation in surplus production

Maximum likelihood

In the analysis of surplus production using the Pella–Tomlinson model, 8 of 109 stocks showed improvement in the AICc by allowing for depensation. The data and model fits for these eight are shown in Figure 4.

Bayesian analysis

The posterior distribution of the depensation parameter (Figure 5) shows a similar pattern to that found for recruitment. The pelagic and demersal stocks show no support for values greater than 0.04 and also have a modal value near zero. The invertebrates with a smaller sample size do not rule out values below 0.1. There is only a single population in the sharks, rays, and skates, and whereas the mode is near $q = 0$, the data are not particularly informative.

All the Markov chains had matching distributions on the ends in the Geweke diagnostic. The samples were again larger than that suggested in the Raftery and Lewis diagnostic calculation. The Heidelberg and Welch diagnostic indicated that each Markov

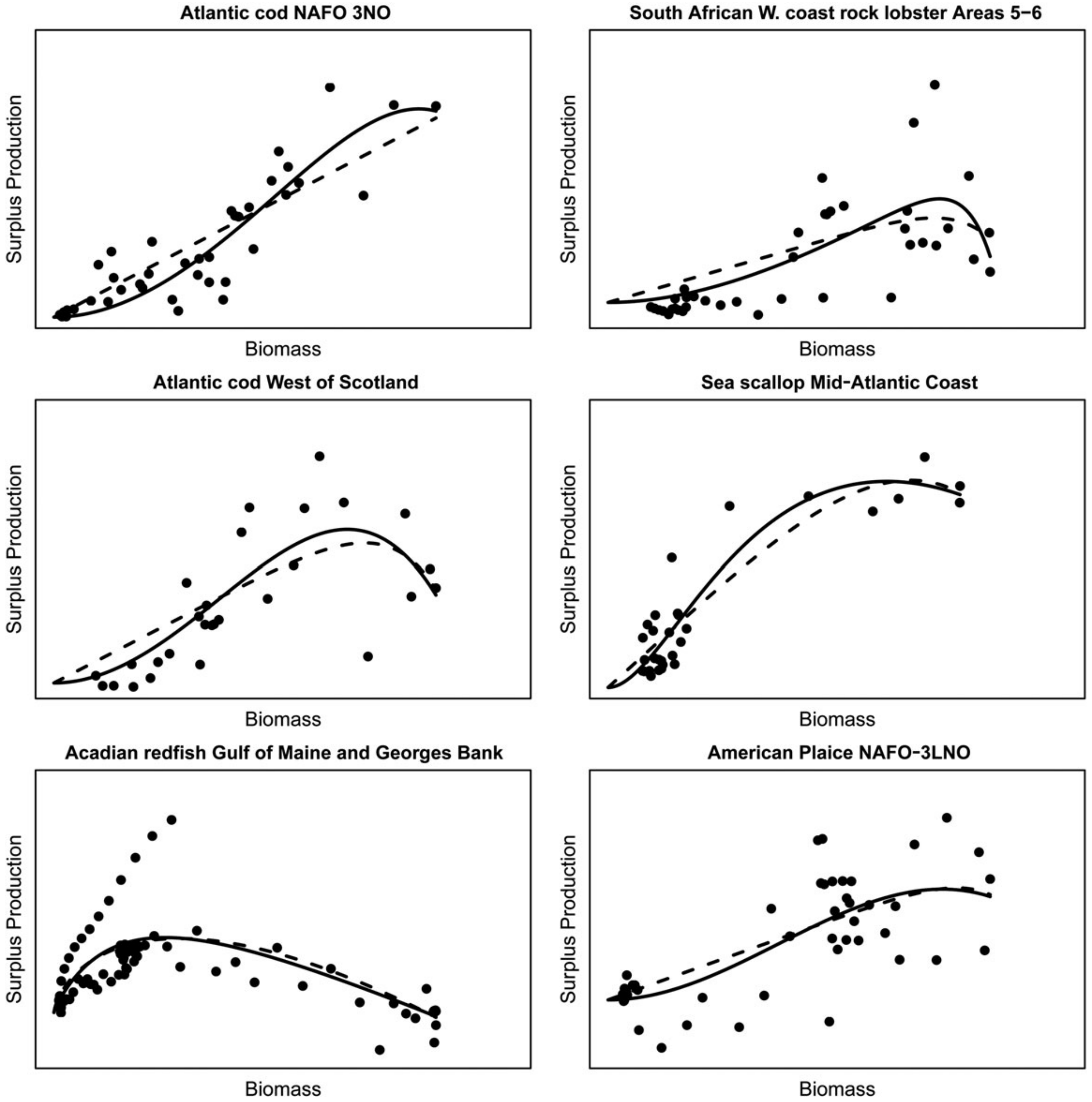

Figure 4. The surplus production data and fits for the eight stocks with improved AICc scores for the depensatory model. The dashed line is the model without depensation and the solid line is the model with depensation.

chain came from a stationary distribution. There was virtually no autocorrelation and the distribution was well mixed.

Sensitivity to recruitment assumptions

One concern about using recruitment and spawning-stock biomass estimated from models as inputs to a statistical analysis is they are both model outputs, and in some cases, there was a spawner–recruit relationship used in estimating the recruitment. To test this, we repeated our Bayesian spawner–recruit analysis using only the datasets from Europe (24 stocks) where the stock assessments do not make any assumption about the spawner–recruit relationship. We found no significant difference in the results for these stocks compared with the entire sample.

Empirical rates of change

Figure 6 shows the probability of stock increase (or decrease) as a function of relative stock size and fishing pressure. The results look remarkably like that expected from the logistic growth model. When stocks are down and to the left of the equilibrium isocline, populations will increase more often than decrease and as the abundance goes lower, and the fishing pressure is decreased, the probability of increase becomes near 1. For example, the lower left hand corner represents $U/UMSY < 0.2$ and $B/BMSY < 0.2$, and

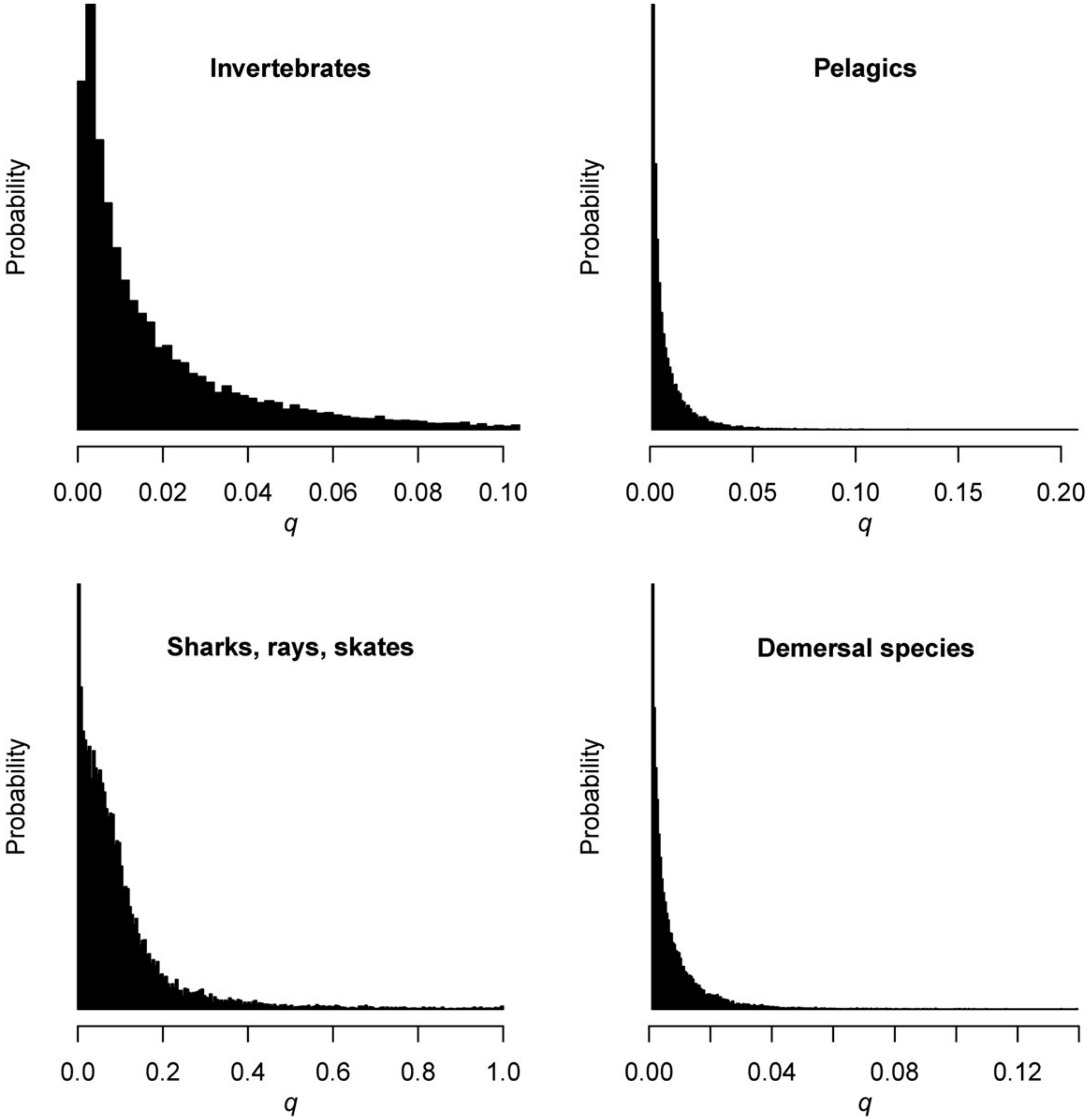

Figure 5. Posterior predictive distribution of the depensation parameter from the surplus production model for four taxa.

there were 84 occurrences of stocks in that region and 82% of the time the stock increased.

Discussion

Depensation

These results largely confirm the earlier work of Myers *et al.* (1995), Liermann and Hilborn (1997), and Keith and Hutchings (2012) that there is little evidence for depensation in stock and recruitment, and this is supported by the surplus production analysis where again little support for depensation was found. Although some stocks do have AICc improvement with the depensatory models, some misclassification due to chance alone would be expected. If we were to cast the analysis in terms of hypothesis testing using the likelihood ratio test, then at the $p > 0.05$ level of significance, two stock–recruit datasets and four surplus production datasets show a significant depensation parameter. Thus, we observed fewer stocks with significant depensation than we would expect by chance alone.

The frequency with which stocks are at low abundance is important for both the ability to detect depensation and the concern about depensation. Neubauer *et al.* (2013) suggest that the amount of time stocks are at low stock size is also important. If stocks rarely go to low stock size, we would be unlikely to detect depensation, but we would also be less concerned about depensatory dynamics. Within the range of spawning stock or total biomass below 20% of the

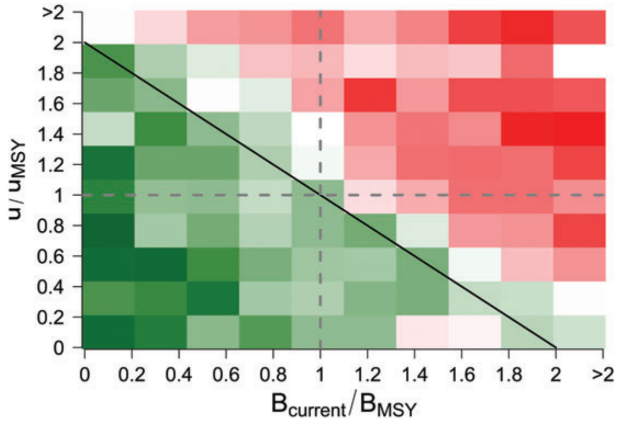

Figure 6. Empirical probability of increase as a function of fishing pressure (*y*-axis) and relative stock size (*x*-axis).

maximum, there was a reasonably uniform distribution of the lowest level observed, and for both recruitment and surplus production, we found some occurrences of stocks as low as 1% of the highest abundance.

Empirical rate of increase analysis

The analysis of rates of increase as a function of fishing pressure and stock size provides the same overall picture. When stocks are at low abundance and when they are exploited at a lower rate, they are more likely to increase. At low fishing pressure and low abundance, stocks almost always increased in abundance just as predicted by non-depensatory models.

Low-density dynamics

Concern about low-density dynamics is imbedded in the concept of stock collapse. Francis and Shotton (1997) defined collapse as reduction to low abundance and failure to recover despite reductions in fishing pressure. Worm *et al.* (2009) and Neubauer *et al.* (2013) defined collapse as $<$0.2 BMSY. Many fisheries agencies have management objectives are to maintain stocks at or above the level that produces maximum sustainable yield, which is generally in the realm of 26–46% of the unfished stock size (Thorson *et al.*, 2012). Thus, management policies that are successful in maintaining this level of abundance are unlikely to push stocks into a realm where depensation might occur. Our work suggests that falling below a depensatory population threshold should not be a major concern for management of stocks, but there are many reasons low population sizes should be avoided including lost potential yield, economic profitability, and employment.

Limitations

The ability to detect depensation depends to a great extent on the amount of data taken from low abundance populations. There certainly are many more stocks that have been observed at low abundance available to us now than there were in the analyses done in the 1990s, but still our sample is small. There is also the concern that populations that might show strong depensation were fished to commercial extinction and do not appear in our dataset. Stocks need to have been commercially important in the last 30 years to have assessments available to us.

We chose to use only stocks that had been depleted at some point to below 20% of their maximum observed stock size. In an AICc analysis, there is a trade-off between the number of stocks and the power of the test, choosing a lower threshold such as 10% would have made the probability of detecting depensation if it is present higher but with a smaller sample size. In the Bayesian analysis, the cut-off level is unimportant, and stocks that were never depleted have no influence on the final result.

The model we used was derived by modelling the dynamics of fertilization assuming random encounters between males and females, and it provides one functional form of a model that shows depensation but certainly other forms are possible as evidenced by the forms used in Myers *et al.* (1995) and Liermann and Hilborn (1997). Given that all three depensatory models lead to similar conclusions, we believe that our conclusions are robust to the specific model form assumed, but it would be useful to model a broad range of depensatory mechanisms from first principles and see if the inference made differs.

The structure of some of the stock assessments used in this analysis may influence recruitment estimates and thus impact meta-analyses such as this one. The original stock–recruitment database developed by Myers *et al.* (1994) was composed largely of outputs from backward projection models (virtual population analysis) in which no stock–recruitment relationship is specified. In contrast, more than half of the assessments in the RAM Legacy Stock Assessment Database that include recruitment estimates come from forward-projection statistical catch-at-age models (Ricard *et al.*, 2012). Such models typically specify the form of the stock–recruitment relationship, but provide substantial flexibility for annual recruitment to differ from the prediction. Nevertheless, recruitments from such models are not free of influence from the assumed model and this influence must be considered when interpreting the results of meta-analysis. The fact that recruitments from the RAM Legacy Database are generally better explained by a regime shift model than a stock–recruitment relationship (Vert-pre, 2013) suggests that the influence of the specified stock–recruitment relationship is minimal, i.e. the estimated recruitments are largely independent of the model specified in the stock assessment.

Conclusions

Within the range of stock sizes for which we have data, there is little evidence that depensatory processes operate. Few populations for which we have data have been pushed to very low levels (1% of unfished biomass) and we cannot rule out depensation at such stock sizes. We have a very small sample of sharks, rays, and skates and using those data alone we really can say nothing about depensation in those taxa. If we believe that their dynamics are closely related to the taxa with large sample sizes then depensation would likely be of little concern, but their life histories are quite different and they may not have similar dynamics to pelagic and demersal fish.

All evidence points to fishing mortality being the key to stock recovery, when fishing pressure is reduced stocks almost always increase in abundance. However, all stakeholders must recognize that environmental changes can have major impacts on stock recovery and expected time and amount of rebuilding.

Acknowledgements

This research was supported by the National Science Foundation and NOAA through the CAMEO (grant numbers 1041570 and 1041678), the Walton Family foundation, and the University of Washington. We owe a large debt to the many people who have contributed to the RAM Legacy Database.

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Handling editor: Howard Browman

ICES Journal of Marine Science

International Council for the Exploration of the Sea
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ICES Journal of Marine Science (2014), 71(8), 2152–2157. doi:10.1093/icesjms/fst179

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Review Article

Renaissance of a caveat: Allee effects in marine fish

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Hutchings, J. A. Renaissance of a caveat: Allee effects in marine fish. – ICES Journal of Marine Science, 71: 2152–2157.

Received 17 July 2013; accepted 18 September 2013; advance access publication 14 November 2013.

The population dynamics of marine fish at low abundance has long been of interest. One century ago, Johan Hjort drew attention to the importance of understanding "the laws which govern the renewal of the animal population". Integral to the current work on the recovery of collapsed fish stocks is the association between abundance and per capita population growth rate (r), a negative correlation being representative of compensation and a positive correlation indicative of an Allee effect, also termed depensation. Allee effects are predicted to slow the rate, and increase the uncertainty, of recovery. Based on studies having sufficient data at low abundance, the magnitude of depletion experienced by some fish populations appears to have been sufficient to have generated either an Allee effect or a transition from strong to weak (or absent) compensatory dynamics. To a first approximation, empirically based Allee-effect reference points are consistent with suggested thresholds for overfishing and stock collapse. When evaluating Allee effects in marine fish, it is important not to conflate causal mechanism(s) with the pattern between r and abundance; the latter is of greater practical import. An additional caveat is that the longer a population remains at low abundance, the more likely it is that the environment around it will change in ways that are unfavourable to recovery. It might be this "temporal tyranny" of small population size that is most likely to produce an emergent Allee effect and depensatory dynamics in some collapsed marine fish populations.

Keywords: depensation, population growth rate, rebuilding, recovery, reference point, threshold.

A scientific legacy predicated by uncommon breadth

In 1947, Johan Hjort delivered a lecture to the Danish Academy of Natural Sciences entitled "Renaissance of the Individual". It was intended to place his fish research of the early 20th century in the context of his more recent international fisheries and whaling work. The lecture comprised his final publication (Hjort, 1948). In addition to Hjort's personal reflections on the work for which he is best known (Hjort, 1914), the essay is of interest because of the impressive job that he does in weaving together ideas from a broad range of thinkers: Plato, Malthus, Lamarck, Darwin, Goethe. From a social-science perspective, Hjort (1948) emphasizes the importance (the "renaissance") of the individual in the context of both human and fish populations, continuing a narrative evident in his writings in the 1930s (Hjort, 1934, 1935).

Hjort was influenced by a palette of classical ideas atypical of contemporary fisheries science. These ideas contributed to a plethora of interests that sculpted a highly influential legacy to marine fisheries research. Foremost among these are his studies of environmentally driven changes in fish abundance, predicated in particular by his work on Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). In 1914, he posited two key ideas (Hjort, 1914, 1948). One of these was that changes in abundance can be greatly influenced by fluctuations in the marine realm (Hjort, 1914), a conclusion stemming from what he had interpreted (Hjort, 1948) to be a lack of association between catches of cod (a presumed metric of abundance) and numbers of fishers (a presumed metric of fishing pressure). A second idea that fish abundance can be significantly influenced by the strength of relatively few year classes, or cohorts, lead him to hypothesize that the primary cause of interannual changes in cohort strength was changes in the abundance of the phytoplankton and zooplankton upon which newly hatched fish larvae depend for food during their "critical period" of early life (Hjort, 1914, 1948).

The question of whether population abundance, in addition to the environment, affects per capita population growth rate (r) is of basic importance to fish population dynamics. Hjort appears to have acknowledged its relevance, noting that "it must be of the greatest importance to ascertain the nature of the laws which govern the renewal of the animal population" (Hjort, 1914). His interest in population dynamical studies matured with his experience on the International Whaling Commission (Hardy, 1950) and revealed an impressive awareness of recently published research on taxa far removed from fish and marine mammals (Richards, 1928; Klem, 1933). In 1935, for example, he used sigmoidal population growth curves of bacteria to inform changes to, and the threat of overfishing in, the Norwegian whaling industry, noting that "the future of a population may best be predicted by studying the fate of the average individual" whose "standard of life" might best be represented by the "rate of [population] growth" (Hjort, 1934, 1935). Hjort's interest in the renewal of animal populations and of how the population growth rate is related to abundance might be said to have foreshadowed research, initiated half a century later, on factors affecting the recovery of depleted marine fish.

Allee effects and depensation

Few would argue against the assertion that overfishing has been a primary determinant of depletion in marine fish populations (Dulvy *et al.*, 2003). But the question of whether low abundance *per se* is generally of greater influence to population growth following stock depletion than environmental variability is unresolved. One recent study, for example, concluded that although stock abundance was related to stock productivity in almost half of 230 fish populations examined, there were irregular shifts in temporal patterns of productivity that could not be explained by abundance in many stocks (Vert-pre *et al.*, 2013).

Based on Warder Allee's classical work on how "certain aspects of survival values" can increase with density when populations are at low abundance (Allee, 1931, 1938), an Allee effect (often termed "depensation" in the fisheries literature) is "a positive relationship between population abundance (or density) and per capita population growth rate" (Courchamp *et al.*, 1999, 2008; Liermann and Hilborn, 2001; Figure 1). Unfortunately, many definitions exist (Stephens *et al.*, 1999; Lidicker, 2010). Myers *et al.* (1995), for example, defined an Allee effect as the difficulty in finding mates, a definition that conflates cause with pattern. Attempts to partition the fitness consequences of Allee effects can be similarly unhelpful. Some authors (Stephens *et al.*, 1999) distinguish "component" Allee effects (a positive association between a "single" component of fitness and abundance) from "demographic" Allee effects (a positive association between "overall" individual fitness and abundance; in fisheries terminology, mean overall individual fitness is analogous to population productivity, r). But this distinction seems unwise from a conservation and management perspective, unless one accepts the doubtful assumption that an increase in one component of fitness automatically leads to an increase in overall fitness. The assumption is unlikely to be true because of the trade-offs ubiquitous among fitness-related traits (Roff, 2002) and the non-depensatory factors that can also affect per capita growth (Liermann and Hilborn, 2001).

An Allee effect is simply a pattern in data. It neither identifies nor implies any particular causal mechanism for generating depensatory dynamics, such as reduced probability of fertilization or finding a mate, impaired group dynamics (e.g. reduced antipredator vigilance), predator saturation, increased incidence of inbreeding or genetic drift, or group conditioning of the environment (Stephens and Sutherland, 1999; Liermann and Hilborn, 2001; Lidicker, 2010). Disentanglement of pattern from causal mechanism would clarify the discussion of Allee effects and its potential importance in marine fish dynamics. Another useful point of clarification is that although an Allee effect can retard the rate and increase the uncertainty of recovery (Kuparinen *et al.*, in press), it need not prevent recovery.

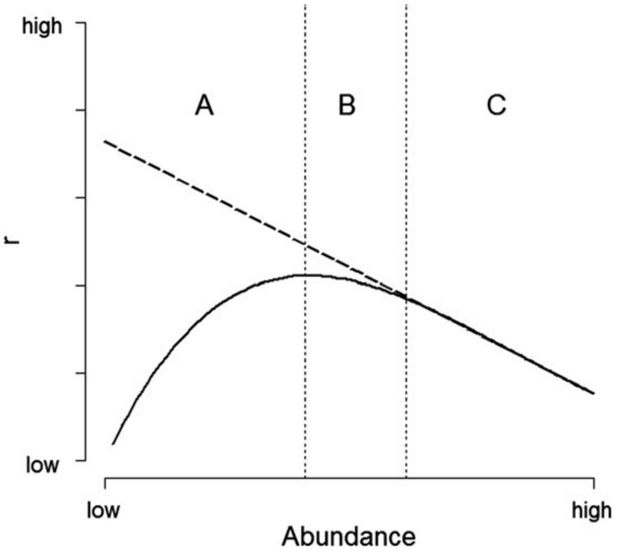

Figure 1. Hypothesized relationship between metrics of r (per capita population growth rate) and abundance. The long-dashed line indicates an unchanging level of compensatory population dynamics and is what is typically assumed in fisheries dynamics models. The solid line reflects changes in the pattern between r and abundance at different levels of abundance [(A) Allee effect or depensation; (B) Allee transition region (weakening compensation); (C) strong and consistent compensation]. The vertical short-dashed lines partition the three patterns of change.

Why are Allee effects considered unlikely in marine fish?

Allee effects are not considered to be of general importance to marine fish population dynamics, despite the caution that has been expressed in rendering such a position (e.g. Liermann and Hilborn, 1997, 2001; Frank and Brickman, 2000; Hutchings and Reynolds, 2004). There would appear to be several reasons for this conclusion.

The first is that two prominent meta-analyses in the 1990s provided little evidence of depensation. Myers *et al.* (1995) examined stock and recruitment data for 128 marine and anadromous fish populations and estimated the value of a parameter (associated with a modified Beverton–Holt model) intended to describe the curvature of the best-fit model to recruitment data at low levels of stock abundance. Of the 26 datasets considered to have sufficient power to detect depensation, only three of them did so, and the only one of these three that was a marine species was the Icelandic spring-spawning herring.

The second meta-analysis employed a Bayesian hierarchical modelling approach to the same dataset. Liermann and Hilborn (1997) reported that the probability distributions of a parameter they used to detect an Allee effect were sufficiently broad to lead them to conclude that one cannot discount the possibility that fish population dynamics are affected by depensation. In other words, difficulties in detecting depensation should not lead one to conclude that depensatory dynamics are rare and unimportant (Liermann and Hilborn, 2001).

In addition to the non-confirmatory nature of these two meta-analyses, there are comparatively few experimental or single-species studies of Allee effects in marine fish, either because these effects have been little-studied or because of a bias against publishing "negative" results (the latter seems unlikely, given that such analyses are prevalent in the non-fisheries literature, e.g. Sæther *et al.*, 1996; Gregory *et al.*, 2010).

General reviews, for example, have documented little evidence of the causal mechanisms of Allee effects in marine fish, e.g. Gascoigne and Lipcius (2004) and Lidicker (2010). Although the impression left by Kramer *et al.* (2009) is that Allee effects have often been found in fish, the studies themselves were not cited, rendering the basis for the assertion, and the extent to which they apply to marine fish, unclear. Berec *et al.* (2006) and Gascoigne *et al.* (2009) cite potential examples in Atlantic cod: laboratory evidence for reduced fertilization success at low densities (Rowe *et al.*, 2004) and altered interspecific interactions (predation, competition) concomitant with low adult abundance (Walters and Kitchell, 2001). The latter, sometimes termed a "cultivation effect", has been linked to slow or absent recovery in cod (Swain and Sinclair, 2000; Frank *et al.*, 2011) and implicated as a potential source of Allee effects in white hake (*Merluccius capensis*; Vergnon *et al.*, 2008). Liermann and Hilborn's (2001) review identified two studies of marine fish (Brock and Riffenburgh, 1963; Steele and Henderson, 1984) that provide circumstantial evidence that increased abundance reduces predation mortality in schooling, pelagic fish. And Stephens and Sutherland's (1999) sole example of a marine fish draws attention to laboratory work on pollock (*Pollachius virens*) which suggests that these advantages to schooling might also apply to demersal species (Rangeley and Kramer, 1998).

Absence of evidence does not constitute evidence of absence

As alluded to previously, a third reason for the perceived lack of importance of Allee effects in marine fish can be attributed to data limitations. Liermann and Hilborn (1997) cautioned that high data variability and few observations at low spawner levels might contribute to the perception that depensation is not possible in marine fish. Myers *et al.* (1995) attempted to account for these data limitation by estimating the statistical power of detecting depensation in their data. Of 128 time-series, only 15 were deemed to provide sufficiently high statistical power in marine fish (11 other datasets having sufficient power represented two species of salmon). After detailing what they perceived to be computational problems in how Myers *et al.* (1995) had estimated statistical power, Shelton and Healey (1999) concluded that depensation will be difficult to detect unless the depensation effect, as reflect by Myers *et al.*'s (1995) parameter, is substantive. They also noted the inherent difficulty in detecting depensation when there is a paucity of spawning-stock biomass (SSB) data at low stock sizes and when time-series are comparatively short [i.e. less than 30 years; Myers *et al.* (1995) and Liermann and Hilborn (1997) applied a 15-year minimum to the data they analysed].

In a similar vein, based on a meta-analysis of time-series abundance data for insects, birds, mammals, and fish, Gregory *et al.* (2010) reported that support for models of both negative (compensation; Figure 1) and positive (Allee effect) density feedback increased with data availability at low population sizes. Another caveat related to data quality is that stock and recruitment data aggregated across multiple substocks can fail to detect Allee effects, although each of the substocks exhibits them (Frank and Brickman, 2000).

Allee effect thresholds and the Allee transition region

In an attempt to overcome some of these data limitations, Keith and Hutchings (2012) analysed a larger dataset (207 marine fish populations) that included longer average time-series for each stock (median period was 32 years) and that encompassed periods of time during which many stocks had remained at low stock levels, thus increasing the number of datapoints at abundance levels at which Allee effects might be evident. Based on the results of a Bayesian hierarchical model, they reported that: (i) many stocks (such as those of Atlantic herring) exhibit strong compensatory population dynamics, meaning that recruits-per-spawner (a strong correlate of *r*) always increased as SSB declined; (ii) others exhibit little or no compensation at low stock size; and (iii) some stocks for some species exhibit patterns in stock size and recruitment consistent with the pattern of an Allee effect.

The meta-analysis by Keith and Hutchings (2012) provided some guidance in identifying a "threshold" level of abundance below which an Allee effect, if present, is likely to be detected. When compensation was weak or absent and when Allee effects were detected, they found that SSB was usually less than 10% of the maximum value observed (SSB_{max}; Figure 2). This is not unlike the "threshold" values (although these lacked an empirical basis) used by Fowler and Baker (1991) in their analysis of Allee effects in large mammals (also 10%) and by Sæther *et al.* (1996) in their analysis of birds (15%). If a $<0.10\ SSB_{max}$ criterion had been applied to the dataset used by Myers *et al.* (1995) (and by Liermann and Hilborn, 1997), very few time-series would have met this data restriction. Of the 15 time-series for marine fish for which statistical power was deemed sufficient to detect depensation (Myers *et al.*, 1995), only 8 (representing four species) contained at least five SSB estimates at $<0.10\ SSB_{max}$ (four time-series contained no SSB data at $<0.10\ SSB_{max}$). By comparison, in the temporally

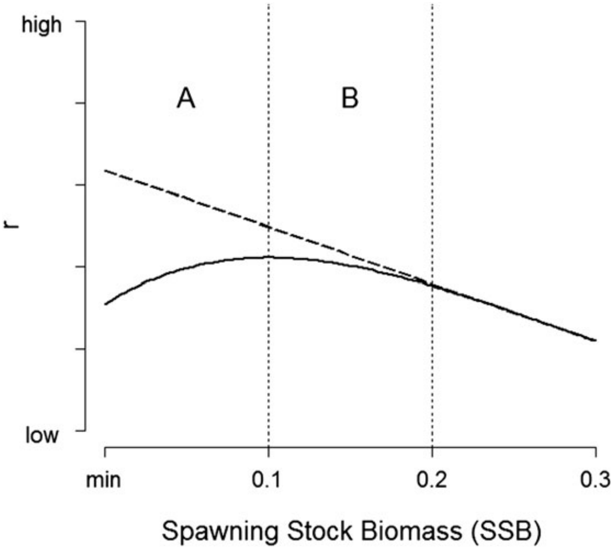

Figure 2. Relationships between *r* (per capita population growth rate and related to recruits per spawner) and SSB, showing suggested abundance thresholds for the Allee effect (A) at $0.10\ SSB_{max}$ and the Allee transition region (B) at $0.20\ SSB_{max}$.

and spatially expanded data analysed by Keith and Hutchings (2012), SSB estimates of <0.10 SSB_{max} were available for 26 species, 19 of which included at least 5 datapoints.

In addition to documenting an Allee effect in some populations, the analysis by Keith and Hutchings (2012) yielded the disconcerting observation that compensatory population dynamics at low stock sizes were not evident in 39 of 104 marine fish species. As reflected by recruits per spawner (R/S) increasing very slowly or not at all with declining SSB (Figure 1B), a lack of strong compensation was not always manifested by an Allee effect, as would be demonstrated by R/S declining with declining SSB (Figure 1A). This outcome suggests that, for some populations, there is an abundance threshold greater than the Allee-effect threshold at which populations enter what Keith and Hutchings (2012) termed an "Allee transition region" (Figure 1B). An Allee-transition threshold would identify an abundance below which the population dynamics of some populations transition from strong compensatory dynamics through density-independent dynamics and, potentially, to levels of abundance at which an Allee effect could be manifested.

Among those stocks for which there was evidence of an Allee transition phase, the weak or absent compensatory dynamics characteristic of the transition region were generally realized at stock sizes less than 0.20 SSB_{max} (Keith and Hutchings, 2012; Figure 2).

Allee effect reference points

Reference points are increasingly used to guide many elements of fisheries management and conservation plans (Hilborn and Stokes, 2010). The SSB thresholds identified above might be described by more generic thresholds, particularly if they were estimated in relation to a commonly applied reference point, such as SSB_{msy}, the SSB at which the maximum sustainable yield is predicted to be obtained. One might argue that SSB_{max} is problematic because it might not be known how representative it is of the unfished biomass or carrying capacity (K) of a given stock. Under the assumption that it underestimates K (fisheries for many stocks often having preceded the collection of SSB data), the thresholds identified here—low levels of relative abundance that should be avoided—would be conservative insofar as a reduction to less than 10% of SSB_{max} would render it highly probable that abundance has declined to less than 10% of K.

The RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012; http://depts.washington.edu/ramlegac/wordpress/) includes data on SSB_{msy} and SSB_{max} (maximum observed value of SSB) for more than 130 marine fish stocks ($n = 135$ at the time of analysis). Excluding the 11 estimates of SSB_{msy} in the database that exceed SSB_{max}, on average, $SSB_{msy} = 0.39\ SSB_{max}$. To a rough first approximation (clearly more sophisticated analyses are possible), the Allee-effect abundance threshold suggested above (0.10 SSB_{max}) would correspond to 0.26 SSB_{msy}, and the suggested Allee-transition threshold (0.20 SSB_{max}) would correspond to 0.52 SSB_{msy} (Figure 3).

Interestingly, these Allee-effect and Allee-transition reference points are not dissimilar to those applied elsewhere for somewhat similar purposes. Neubauer *et al.* (2013), for example, defined a collapsed stock as one that had declined to less than 0.20 B_{msy}. Their work also indicated that collapsed stocks have considerably longer, and highly uncertain, recovery periods when compared to stocks that have declined to lesser degrees. Many jurisdictions, such as the United States and Australia, use 0.50 B_{msy} as the threshold that identifies overfishing (Hilborn and Stokes, 2010).

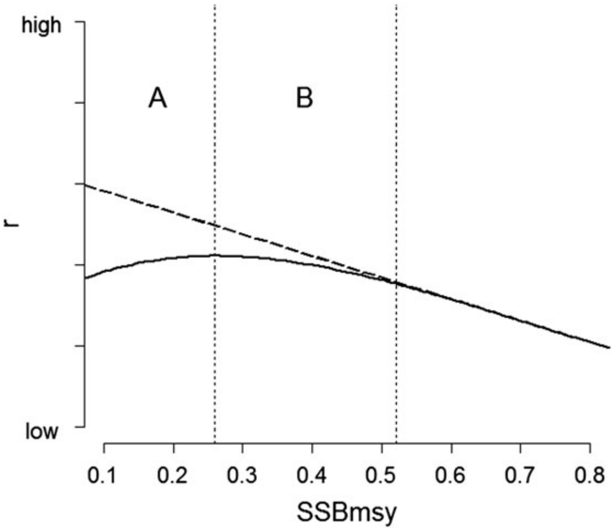

Figure 3. Relationships between r (per capita population growth rate and related to recruits per spawner) and SSB_{msy} (SSB corresponding to maximum sustainable yield), showing suggested reference points for the Allee effect (A) at 0.26 SSB_{msy} and the Allee transition region (B) at 0.52 SSB_{msy}.

The Allee-effect reference points suggested here provide empirical strength, from a population dynamical perspective, to the (arguably) arbitrary reference points articulated elsewhere for stock collapse and overfishing. That is, some stocks that have declined below 0.20 B_{msy} (collapse) and 0.50 B_{msy} (overfishing) might be likely to face increased probabilities of realizing an Allee effect or of entering an Allee transition region, respectively, and thus experiencing reduced probabilities of recovery. Links between fisheries reference points and population-depletion criteria applied by conservation organizations, such as the IUCN (World Conservation Union), have been examined comprehensively elsewhere (Dulvy *et al.*, 2005; Davies and Baum, 2012) and the utility of using both to assess conservation status is amply supported by these studies.

Closing points

There is evidence in some, but not all, marine fish populations that compensatory density-dependence weakens when abundance declines to very low levels (Keith and Hutchings, 2012). Such a weakening in the strength of compensation will increase the uncertainty of recovery in depleted populations, underscoring the diminished ability of small populations in general to persist and grow in the presence of environmental stochasticity (Lande, 1993).

When evaluating the potential importance of Allee effects on the population dynamics of marine fish, the following points merit consideration.

First, mechanisms underlying Allee effects should not be conflated with the pattern of an Allee effect. It is the way in which r changes with abundance at low population sizes that is of primary importance to fishery rebuilding, population recovery, and conservation status, not whether one mechanism or another is responsible for the pattern (although the latter is clearly worth exploring in its own right).

Second, an Allee effect need not prevent recovery (unless, of course, r is negative). Rather, it is predicted to retard the rate of, and increase the uncertainty associated with, recovery (Kuparinen *et al.*, in press).

Third, the abundance thresholds and reference points for Allee effects and Allee transition regions suggested here lend support to reference points identified elsewhere for overfishing and population collapse, providing additional reasons to fishery managers for why these regions of fish stock abundance should be avoided.

Fourth, it seems important to distinguish the passing of a threshold or reference point pertaining to an Allee effect from the period that a population spends at such low abundance (note that persistence at low abundance can be a product of low *r* coupled with environmental stochasticity; it need not reflect the attainment of a stable equilibrium). It might well be that the passing of an Allee-effect threshold by a population for a short period, relative to that population's generation time, will in itself not be sufficient to generate a reduced rate of recovery.

But logic dictates that the longer a collapsed population remains at low abundance, the more likely it is that the environment around it will change, quite possibly in ways that are unfavourable to the growth and the recovery of the depleted population (Swain and Sinclair, 2000; Brander, 2005; Benoît and Swain, 2008; Swain, 2011; Audzijonyte *et al.*, 2013). Changes in the abundance of interacting species to which an increasingly depleted population becomes increasingly vulnerable can lead to what has been termed an "emergent" Allee effect (*sensu* Courchamp *et al.*, 2008; Hutchings and Rangeley, 2011). One example of an emergent Allee effect would be reductions in *r* of a depleted population resulting from increases in predator abundance to which the prey's *r* would not otherwise have been affected if the predator abundance had not increased (see Swain, 2011, for a potential example). This is one of the tyrannies of small population size. The longer a population remains small, the longer, and more uncertain its recovery (Lande, 1993; Neubauer *et al.*, 2013), particularly when Allee effects are present (Kuparinen *et al.*, in press). Methodologically, a stock:recruitment analysis may be of limited utility as a means of detecting depensation if emergent Allee effects increase adult mortality (thus reducing *r*) as SSB declines, but do not affect *R/S*.

Hjort's (1914) attention to understanding the factors affecting the renewal of marine fish populations, notably within the context of the population growth rate (Hjort, 1934, 1935), has particular import to the study of recovery in depleted marine fish, a subject of enquiry that has increased during the past 20 years (e.g. Hutchings, 2000; Worm *et al.*, 2009; Murawski, 2010; Lotze *et al.*, 2011; Neubauer *et al.*, 2013). Among the hypothesized correlates of recovery, a key one pertains to population dynamics at low abundance. The slow or absent recovery currently observed for some marine fish populations provides an appropriate empirical template against which a renaissance of the caveat of the Allee effect might be fruitfully considered.

Acknowledgements

I thank Howard Browman for the opportunity to write this manuscript, the Natural Sciences and Engineering Research Council of Canada for support in the form of a Discovery Grant, and the Hämeen Vajatoimisto for office space. I am grateful to Anna Kuparinen and two anonymous referees for their very helpful comments on earlier versions of the manuscript.

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Handling editor: Sarah Kraak

ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2158–2170. doi:10.1093/icesjms/fsu063

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations

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Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. – ICES Journal of Marine Science, 71: 2158–2170.

Received 28 October 2013; revised 11 March 2014; accepted 13 March 2014; advance access publication 24 April 2014.

Hjort (1914. Fluctuations in the great fisheries of northern Europe. Rapport et Procès-Verbaux des Réunions du Conseil Permanent International pour l'exploration de la Mer, XX: 1–228) identified two important aspects of the early life of fish as being important determinants of fluctuations in year-class strength: changes in nutrition and transport. He dismissed a third possible influence, changes in the abundance of the reproductive stock. Here, we describe how a recently discovered characteristic behaviour of age-structured populations termed *cohort resonance*, which does involve changes in adult abundance, can have a substantial effect on fluctuations in fished populations. Cohort resonance involves selectively greater sensitivity of age-structured populations to generational frequencies and to very low frequencies in the environmental signal influencing a population. This frequency-dependent selectivity has been shown to increase with fishing, as do the total amounts of variability in recruitment, egg production, and catch. Cohort resonance differs from other recent model mechanisms proposed to explain the observed increase in variability with fishing in that it does not require over-compensatory density-dependence. It stems from the compensatory ascending limb of the egg–recruit relationship, and is a characteristic of a stable population driven by a random environment. We demonstrate the differences in frequency selectivity and increases in variability with fishing among three different Pacific coast species with different longevity: coho salmon (*Oncorhynchus kisutch*; ∼3 years), Pacific hake (*Merluccius productus*; ∼25 years), and Pacific Ocean perch (*Sebastes alutus*; ∼90 years). The shortest lived, coho salmon is the most sensitive to environmental variability, but variability in egg production and catch both increase more rapidly with fishing in the longer-lived species. Understanding cohort resonance will aid in anticipation of predicted potential changes in the frequency content of the physical environment with changing climate (e.g. more frequent El Niños), and it provides a warning regarding the possible confounding of increasing sensitivity to slow change due to fishing with actual slow change of population parameters due to climate change. Our understanding of the role of cohort resonance in population variability will be enhanced by further identification of empirical examples. We describe some of the challenges in this effort.

Keywords: age structure, environmental variability, fishing, frequency response, stochastic models.

Introduction

The problems facing Hjort and his fishery science colleagues in 1914, even in the early years of fisheries science, involved the same topics as those facing fishery scientists in 2014. We still seek to understand the causes of fluctuations in fished populations, but with added concern for anticipated effects of a changing climate due to increasing CO_2 concentrations in the atmosphere. Hjort (1914) presciently defined this field as we know it by focusing research on the early lives of fish, and by proposing two reasons for dramatic variability in their survival: nutrition and transport. These have had a great effect on fisheries research since then, leading to two of the dominant mechanisms proposed to underlie interannual variability in recruitment (Houde, 2008). The former has become well known as the "match–mismatch" mechanism (Cushing, 1990), and the latter underlies the "stable retention" mechanism (Iles and Sinclair, 1982).

Here, we describe a mechanism related to a conclusion by Hjort (1914) that is less well remembered. In the paragraph preceding his description of the nutrition and transport effects, he considered the role of variability in egg production by adults as an effect on variability in recruitment. He concluded that, "it is difficult to avoid the conclusion that the actual quantity of eggs spawned is not a factor in itself sufficient to determine the numerical value of a year class." Currently, we, of course, include an underlying effect of stock on recruitment, and take careful note of maternal effects, but we seldom focus on their role in interannual variability. However, here we describe the developing understanding of cohort resonance (Bjørnstad *et al.*, 2004; Worden *et al.*, 2010), a mechanism that has a substantial influence on the annual fluctuations in the number of recruits in a year class, and does involve variability in annual egg production. Our results indicate why it is not surprising that Hjort (1914) concluded that the amount of egg production each year had no influence on the dynamics of interannual variability in cohort abundance. This mechanism also involves another aspect of population dynamics on which Hjort recommended more research, age structure, though his interest lay in the prediction of yield from older ages based on the abundance of the young, rather than in the role of age structure in population dynamics.

Cohort resonance was described as an integrated, whole mechanism by Bjørnstad *et al.* (2004), though various aspects had been alluded to earlier. They showed that the peaks at low frequencies (i.e. decadal scale variability) and frequencies near 0.4 cycles per year seen in the calculated spectrum of the catches of cod in the Skagerrak were not dominant frequencies of the variable environment, rather they were peaks in the sensitivity of the age-structured cod population to environmental variability. This meant that populations could be viewed as filters that are more sensitive to some frequencies of environmental variability than others (Greenman and Benton, 2005). In particular, models of age-structured populations exhibit peaks in sensitivity to low frequencies and generational frequencies when driven with white noise (i.e. equal variance at all frequencies). The term "sensitivity" in this context refers to the ratio of the variance at a certain frequency in an output, such as abundance or recruitment, to the variance at that same frequency, in the input being varied by the environment, such as survival at age 1. This sensitivity is a function of frequency [or equivalently, a function of period = 1/(frequency)]. They drew attention to the consequences of sensitivity to low frequencies because that would emphasize slowly varying (decadal) trends, which would confound efforts to detect actual slowly developing changes to life history rates due to climate change (i.e. the *cloaking effect* of cohort resonance). To be clear, we use the term "cohort resonance" here to refer only to sensitivity to: low frequencies and frequencies near 1/(generation time), i.e. our definition does not include variability at frequencies near 1/(2 × generation time), which were also discussed in Bjørnstad *et al.* (2004). Such cycles of period 2 generations have been discussed extensively elsewhere (see Botsford and Wickham 1978; Botsford 1997, and references therein).

The cohort resonance effect was elevated in importance when it was found that both the selective sensitivity to low frequencies and generational frequencies identified by Bjørnstad *et al.* (2004) and the overall sensitivity to environmental variability increased with declining survival. Such a decline in survival could be caused, for example, by fishing or a long-term decline in environmental conditions influencing larval or juvenile survival (Worden *et al.*, 2010). This finding suggested that a better understanding of cohort resonance could address some of the current questions regarding the synergistic effects of fishing and climate change (e.g. Perry *et al.*, 2010; Planque *et al.*, 2010; Hollowed *et al.*, 2011). It could also help to explain the growing empirical evidence of increased population variability with fishing, as seen in time-series of abundance, egg production (Hsieh *et al.*, 2006), and recruitment (Brander, 2005; Ottersen *et al.*, 2006). Cohort resonance could possibly shed light on the various roles of proposed causal factors such as the selective greater reduction in older ages due to fishing, i.e. age truncation (Brander, 2005; Ottersen *et al.*, 2006; Anderson *et al.*, 2008; Planque *et al.*, 2010; Shelton and Mangel, 2011a), maternal effects (Brander, 2005; Ottersen *et al.*, 2006; Planque *et al.*, 2010), and selection for changes in life history by fishing (Law, 2000; Planque *et al.*, 2010).

The prevailing view of the cause of the increase in variability with fishing is that it arises from unstable behaviour of fish populations (Shelton and Mangel, 2011b; Sugihara *et al.*, 2011). Anderson *et al.* (2008) sought to explain the observation that time-series of annual egg production from a number of fish species off the west coast of the United States showed greater variability in fished species than unfished species (Hsieh *et al.*, 2006). They introduced two effects proposed qualitatively to arise from the truncation of an age structure by size-selective fishing, into their non-age-structured model: (i) better tracking of the environmental signal by the population, and (ii) a change in the intrinsic rate of population increase, *r*. From analysis based on fitting general functional forms of the time-series (S-map analysis), and a discrete time model of the dynamics of total abundance having the familiar Ricker (1954) form, they concluded there was limited evidence for the increased tracking as a cause, and strong evidence for changing dynamics due to increased rate of increase, *r*.

In a later study, Shelton and Mangel (2011a) addressed the question of how increased fishing increases variability using a discrete time model of the dynamics of lumped total biomass, with a Ricker (1954) stock–recruit relationship representing the recruits added each year. They noted that literature-based values of the parameters of their model for 45 fish species indicated that models of the species dynamics were typically in regions of parameter space where the populations would not be stable. They showed that in these models: (i) fishing increased variability, (ii) populations were more sensitive to environmental variability in recruitment than in adult mortality, and (iii) temporal correlation in environmental variables played a vital role in determining population variability.

Here, we first describe what cohort resonance adds to the current view of the issues Hjort was addressing. We then note how cohort resonance provides an alternative to the prevailing explanation of the observed increases in variability with fishing. We characterize an important way in which cohort resonance will vary with species, the dependence on longevity. We do this by illustrating the effects of fishing on frequency selectivity and overall variability in three species from the California Current, with different longevity: Pacific ocean perch (*Sebastes alutus*; POP), Pacific hake (*Merluccius productus*; a.k.a. whiting), and coho salmon (*Oncorhynchus kisutch*).

Basic model and previous analyses

To represent the behaviour of these age-structured populations, we used a linear age-structured matrix model with a non-linear egg–recruit relationship. For the iteroparous species (POP and Pacific hake), the model has the form

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ s_1(t)x_1(t) \\ s_2x_2(t) \\ \vdots \\ s_{n-1}x_{n-1}(t) \end{pmatrix}, \qquad (1)$$

where $x_i(t)$ is the number of individuals in age class i at time t.

For the semelparous species (coho salmon), the model takes the form

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ (1-p_1)s_1(t)x_1(t) \\ (1-p_2)s_2x_2(t) \\ \vdots \\ (1-p_{n-1})s_{n-1}x_{n-1}(t) \end{pmatrix}, \qquad (2)$$

where the multiplicative $(1-p_i)$ terms account for the fact that spawning is an additional source of mortality in a semelparous species.

For both of these, $P(t) = \sum_{i=1}^{n} p_i f_i x_i(t)$ is the annual egg production resulting from the age-specific probability of spawning, p_i, and the age-specific fecundity rates, f_i. Recruitment is a Beverton and Holt (1957) function of egg production, multiplied by lognormal random noise,

$$R[P(t)] = \frac{\alpha P e^{-\xi t}}{1+\beta P} \qquad (3)$$

with random values of ξ chosen from a Gaussian distribution with the mean 0.0 and standard deviation σ_R. Survival is a function of instantaneous natural mortality, M_R (age 1) or M (constant over ages >1 year), and age-dependent fishing mortality, F_i', and is given by $s_i = \exp(-M - F_i')$. The methods used to calculate survivals and fecundities are shown in the Supplementary data along with all parameter values.

While we present the model of semelparous coho salmon explicitly in terms of the linked spawning and mortality, in the subsequent analyses presented here none of the differences between species' behaviour is due to the differences between their semelparous and iteroparous life histories. Thus, the responses of the coho salmon here would be the same as those of an iterparous species with the same pattern of the amount of spawning at age.

In previous analyses, we obtained equilibrium conditions for these models and analysed deterministic stability (Worden *et al.*, 2010). Population stability depends on the slope of the egg–recruit relationship at equilibrium. Because we are using a Beverton–Holt stock–recruitment model, whose slope is always positive, the population will always be stable about its equilibrium. It will not display the kind of unstable behaviour in the models currently proposed to be the cause of increasing variability with fishing (Shelton and Mangel, 2011b; Sugihara *et al.*, 2011). Stochastic analysis of this model, however, shows that this locally stable population model can be continuously perturbed away from equilibrium by environmental variability, and will display the sensitivity to specific frequencies of environmental variability characteristic of cohort resonance: low frequencies and generational frequencies (i.e. with period equal to the generation time; Worden *et al.*, 2010). This is an important distinction between cohort resonance and other population dynamic mechanisms underlying cyclic behaviour. Cycles with period 2 generations are caused by over-compensatory density-dependence (i.e. a negative slope in the stock–recruit relationship), and the cyclic state is unstable about the equilibrium. These are the inter-cohort cycles described in Bjørnstad *et al.* (2004), whereas cohort resonance cycles are the intra-cohort cycles.

Qualitative explanation of cohort resonance

The mechanistic basis for cohort resonance, and the way it is related to the studies of Hjort (1914) can be understood based on two graphical representations (Figures 1 and 2). Changes in the long-term equilibrium values of recruitment due to long-term changes such as increased mortality due to fishing are contained in the well-known condition for equilibrium of an age-structured population with density-dependent recruitment (Figure 1, Sissenwine and Shepherd, 1987; Botsford, 1997). This graphical version of the equilibrium condition states that the equilibrium value of recruitment will be at the intersection of the egg–recruit relationship and a straight line through the origin, with slope equal to the inverse of lifetime egg production (LEP, Figure 1). As fishing increases (or survival declines for other reasons), the equilibrium moves the unfished equilibrium [e.g. point (a)] to lower annual egg production and lower recruitment [e.g. point (b)], until the LEP has been reduced to the inverse of the slope at the origin of the egg–recruit relationship, at which point [point (c); and beyond], the equilibrium is zero. For our purposes here, note that as the equilibrium declines, the local slope of the egg–recruit relationship itself becomes steeper with the Beverton–Holt model.

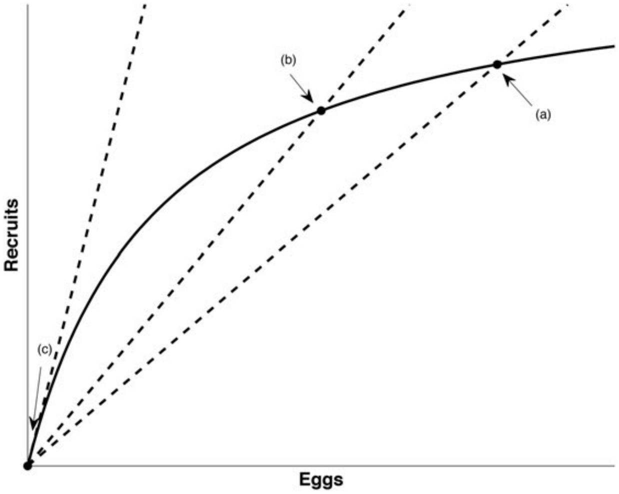

Figure 1. Graphical representation of the equilibrium condition for an age-structured population with density-dependent recruitment. The solid line is the annual number of recruits produced from the annual number of eggs produced. The dashed lines have slope equal to 1/LEP, where LEP is the lifetime egg production of females in the population. For increasing rates of fishing, the slope increases. For example, point (a) could represent the unfished equilibrium, and point (b) an equilibrium with fishing. When the population is fished at a rate that causes the slope to be greater than or equal to the slope of the egg–recruit relationship at the origin, the equilibrium recruitment will be zero [point (c)].

The dynamic behaviour underlying the greater sensitivity of cohort resonant populations to environmental signals on generational time-scales can be understood by considering the case in which the survivals at each age in Equations (1) and (2) are not time varying, and environmental variability is solely in recruitment [Equation (3)]. In that case, the variation in egg production $P(t)$ from its equilibrium value is the weighted sum of past variations in recruitment from the equilibrium recruitment, with the constant weighting factors being the amount of spawning per recruit at that age (i.e. survival to each age times the fecundity at that age; Worden *et al.*, 2010).

With that in mind, we can graphically portray the ways in which variability is transformed as it flows through the population for both the unfished (Figure 2a) and the fished (Figure 2b) case. The recruitment signal (the red signal in the lower left of Figure 2a and b) is a

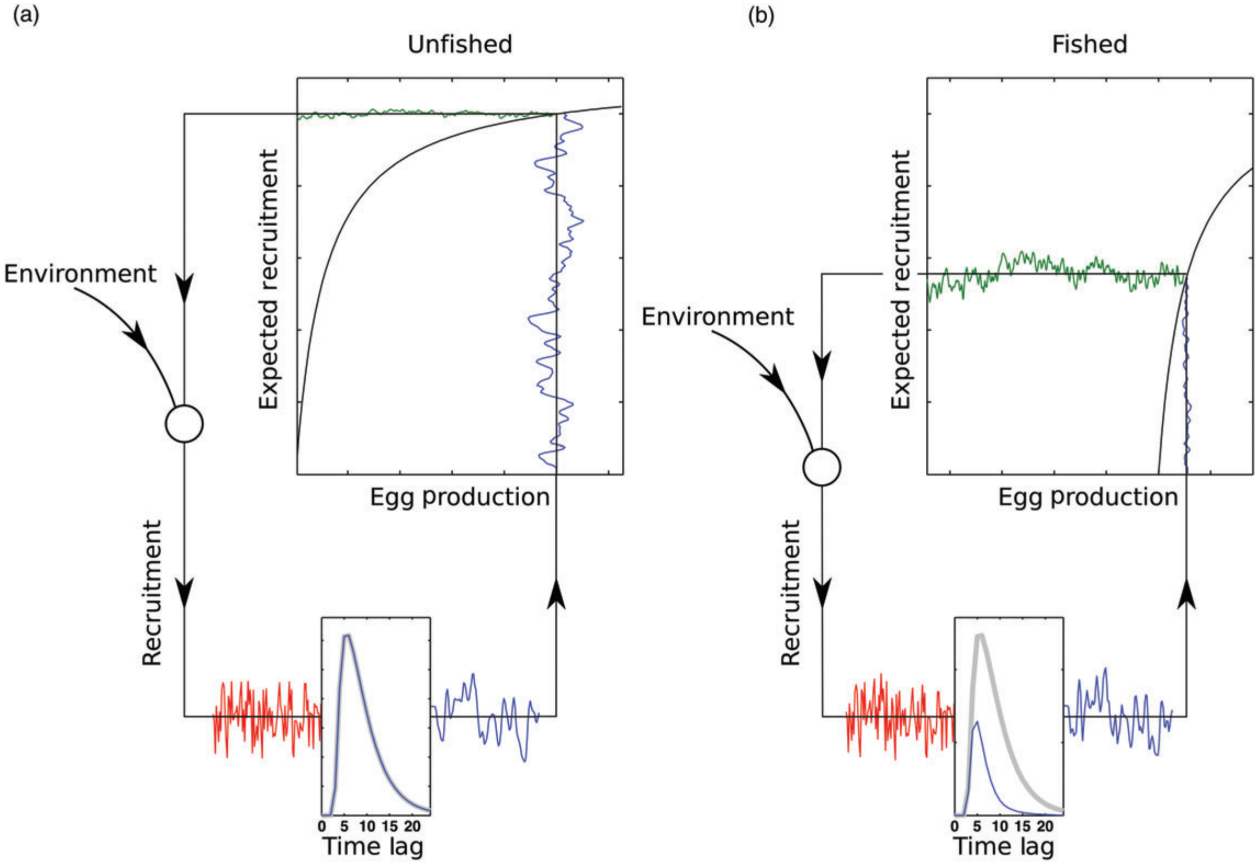

Figure 2. Schematic representation of the variability about equilibrium of signals involved in the cohort resonance mechanism for the unfished case (a) and the fished case (b). In the unfished case (a), the slope of the egg–recruit relationship is shallow, so the variability in expected recruitment can be less than that in egg production. The introduction of environmental variability into this signal produces the highly "noisy" recruitment (red signal) that would be observed empirically. Egg production (purple signal) is the weighted sum of past recruitments. The weighting function, i.e. the product of survival to age times fecundity at age, is shown in the box in the lower part of (a) and (b). The fished case (b) differs in two ways: (i) the slope of the egg–recruit relationship is steeper at the lower equilibrium (as explained by Figure 1), hence the signal is "amplified", and (ii) the distribution of reproduction over age is truncated, leading greater reinforcement of frequencies near the inverse of the peak reproductive age.

combination of the expected recruits from egg production (the green signals in Figure 2a and b) and the multiplicative noise from the environment [Equation (3)]. The egg production time-series (the purple signal in Figure 2) will be less variable than recruitment signal (red) because it will be a weighted sum of the noisy recruitment time-series. The weighting function (spawning at age) is shown in the lower boxes in Figure 2a and b. The effect of that variability in egg production (i.e. the purple signal in the upper part of Figure 2) on recruitment in each later year depends on the slope of the egg–recruit relationship at equilibrium (i.e. the amplification from the purple signal to the green signal will be greater with a steeper slope).

The sensitivity to generational frequencies in the cohort resonant effect arises when the environmental signal has a substantial periodic component with period T, where T is the generation time (contained in the weighting function in the lower boxes of Figure 2). For example, consider the example of a survival time-series that consisted of pulses of favourable recruitment conditions every T years. Signals with that periodicity would tend to be reinforced because the high recruitment from each pulse of high survival would be augmented by the high egg production from the previous pulse T years earlier (i.e. pulses in the green signals in Figure 2 would coincide with new pulses in the environment). One can see intuitively that this effect will be stronger under certain conditions. One condition is when the width of an individual's spawning-at-age distribution (i.e. the function in the box in the lower left) is narrow. This will concentrate the future effects of recruitment into a narrower range of ages, thus focusing the effect increasingly on a single age. The second is when the slope of the egg–recruit function at equilibrium is steep. This will amplify the magnitude of fluctuations (going from the blue to the green signal in the top part of Figure 2). Both the narrowness of the age span of reproduction and the steepness of the slope of the egg–recruit relationship at the origin become stronger as fishing increases; the former is due to age truncation, and the latter is due to the equilibrium moving down to points with steeper slope on the ascending limb of the egg–recruit function. Comparing these effects in the fished case (Figure 2b) with the unfished case (Figure 2a), the narrower spawning age distribution in Figure 2b focuses egg production in fewer ages, and a steeper slope at equilibrium causes variability in egg production (i.e. the purple signal in the top part of Figure 2b) to produce greater relative variability in recruitment (i.e. the green signal).

The other peak in the frequency-dependent sensitivity of cohort resonance, sensitivity to low frequencies, can be viewed as an effect arising from a low level of density-dependence. As fishing increases and the slope of the dashed line in Figure 1 becomes steeper, the population will increasingly resemble a Leslie Matrix (Caswell, 2001) with no density-dependence, i.e. Figure 1 would resemble two straight lines, one with the slope of 1/LEP, and the other with slope equal to the constant egg-to-recruit survival at low abundance. Such a matrix would not have a non-zero equilibrium. If it were subject to random environmental variability in recruitment, it would display the behaviour of a neutrally stable system with λ near 1.0, i.e. it would vary about a constant level on time-scales near the generation time for a while, then wander slowly to a different constant level and vary similarly about that level for a while, etc. Slight random changes in early survival could have a great effect on recruitment if they lasted long enough to produce something like the geometric growth characteristic of these matrices. If they lasted a shorter time, values of λ slightly greater than, and slightly less than 1.0 would tend to cancel. Thus, the population becomes sensitive to lower frequencies. Note that this sensitivity to low frequencies is a consequence of the population having little density-dependence, and λ being near 1.0, thus it is not directly related to the resonance phenomenon.

Expected cohort resonance from three fished species

We can obtain some sense of what to expect from cohort resonance by examining expected results from three fished species with different longevities. These expectations can then be compared with empirical population time-series over the last several decades. Here, we examine three species fished off the US west coast: coho salmon (*Oncorhynchus kisutch*; ~3 years), Pacific hake (*M. productus*; ~25 years), and POP (*S. alutus*; ~90 years), where the value in parentheses is the approximate maximal age. We first outline the differences in spawning age structure and response to fishing, then show how these lead to differences in the frequency responses between species with different longevities. Because of the interest in how variability increases with fishing (Anderson *et al*., 2008; Shelton and Mangel 2011a, b; Sugihara *et al*., 2011), we then compare how variability in recruitment, egg production, and catch increase with fishing.

We compare these three species in terms of their manifestation of the cohort resonance mechanism, in a way that focuses on the effects of differences in age structure. We project the different behaviour of these three species using an age-structured model with different parameters for each species from recent stock assessments (see equations and parameter values in the Supplementary data). Because the cohort resonance mechanism of interest here (i.e. sensitivity to generational frequencies and low frequencies) depends only on the ascending, compensatory part of the stock–recruitment curve, we use a Beverton–Holt egg–recruit relationship (Beverton and Holt, 1957). Stock–recruitment relationships for some species may, of course, have a descending, over compensatory limb at high stock values. Small signal behaviour about equilibria on that declining part of the curve could lead to locally unstable populations with cycles of period 2 generations, and could also exhibit more complex, chaotic behaviour (Hassel *et al*., 1976; Botsford, 1992). We do not address that possibility here because our purpose is to show that such unstable behaviour is not required for variability to increase with fishing. This contrasts with the explanations of the observed increase in variability with fishing by others (Shelton and Mangel, 2011b; Sugihara *et al*., 2011). For the purposes of comparing the effects of the different age structures, we apply the same lognormal random variability in recruitment survival to all three species. The Beverton–Holt egg–recruit relationships are parameterized so that they all have the same asymptotic maximal value of recruitment, and the slope parameters are specified such that the equilibria of the three species will be at the same point when the species have the same value of the fraction of lifetime recruitment (FLEP). FLEP is the ratio of current LEP to unfished LEP, essentially the same as spawning potential ratio in other fishery publications (Goodyear, 1993; Mace and Sissenwine, 1993; O'Farrell and Botsford, 2005). Values of FLEP convey the same information as the values of LEP involved in the equilibrium condition depicted in Figure 1, but they are normalized by dividing by the value of LEP in the unfished condition. This is commonly done to put the persistence of populations of different species on a common, comparable basis, regardless of differences in fecundities, larval survivals, etc. Using FLEP, rather than LEP, also involves the presumption of some greater degree of generality in persistence mechanisms described by FLEP than by the actual values of LEP. Here, we chose the value of the slope at the origin [α in Equation (3)] of the Beverton–Holt function so that all three populations collapse at $\mathrm{FLEP_C} = 0.1$, a reasonable value both locally (Dorn, 2002) and globally (Myers *et al*., 1999).

The cohort resonance effect is determined by the age distribution of reproduction, and the way that distribution changes with fishing (Figure 3a–c). The spawning age distributions of POP, Pacific hake, and coho salmon along the west coast of the United States are dramatically different, but all are truncated by increased fishing, which reduces lifetime reproduction and slightly diminishes the dominant age of spawning.

Lifetime reproduction decreases with increased fishing more rapidly in longer-lived species (Figure 3d) This means that for the Beverton–Holt egg–recruit relationship (Beverton and Holt, 1957), which does not involve over-compensation, fishing will reduce equilibrium recruitment sooner for longer-lived species (Figure 1). Here we compare behaviour of these three species at different values of FLEP, rather than different values of fishing mortality, *F*, to focus more directly on dynamic differences due to age structure, rather than confounding them with differences in equilibrium (which are static, long-term effects, also due to age structure as shown in Figure 3d). Each fishing level is identified by its Exploitation Index, EI ($\mathrm{EI} = (1 - \mathrm{FLEP})/(1 - \mathrm{FLEP_C})$), where $\mathrm{FLEP_C}$ is the value at which equilibrium recruitment collapses to zero, here assumed to be 0.1 for all three species (Sissenwine and Shepherd, 1987). Thus, EI is a convenient common measure of fishing level for the three species, ranging from no fishing ($\mathrm{EI} = 0$) to population collapse ($\mathrm{EI} = 1.0$).

Differences in spawning age structure lead to differences in the environmental frequencies to which different species are sensitive. This effect is demonstrated here with the dominant form of environmental variability found in marine fish, high variability in recruitment survival [Equation (3); Figure 4]. The forcing signal used here was chosen to have equal variance at all frequencies, i.e. it was white noise. Because of that, the quantity plotted in Figure 4 is a measure of how sensitive the populations are to each of the different frequencies of variability in the environment. Our measure of sensitivity here is the ratio of the variance of the particular variable (recruitment, egg production, catch) about its equilibrium value to the variance of the variable that is being forced by the environment (here recruitment survival), about its mean. This variable is the same as what is referred to elsewhere as the power spectrum. Since these are not electrical signals, they do not represent power, so we refer to this variable as frequency-dependent sensitivity of variance.

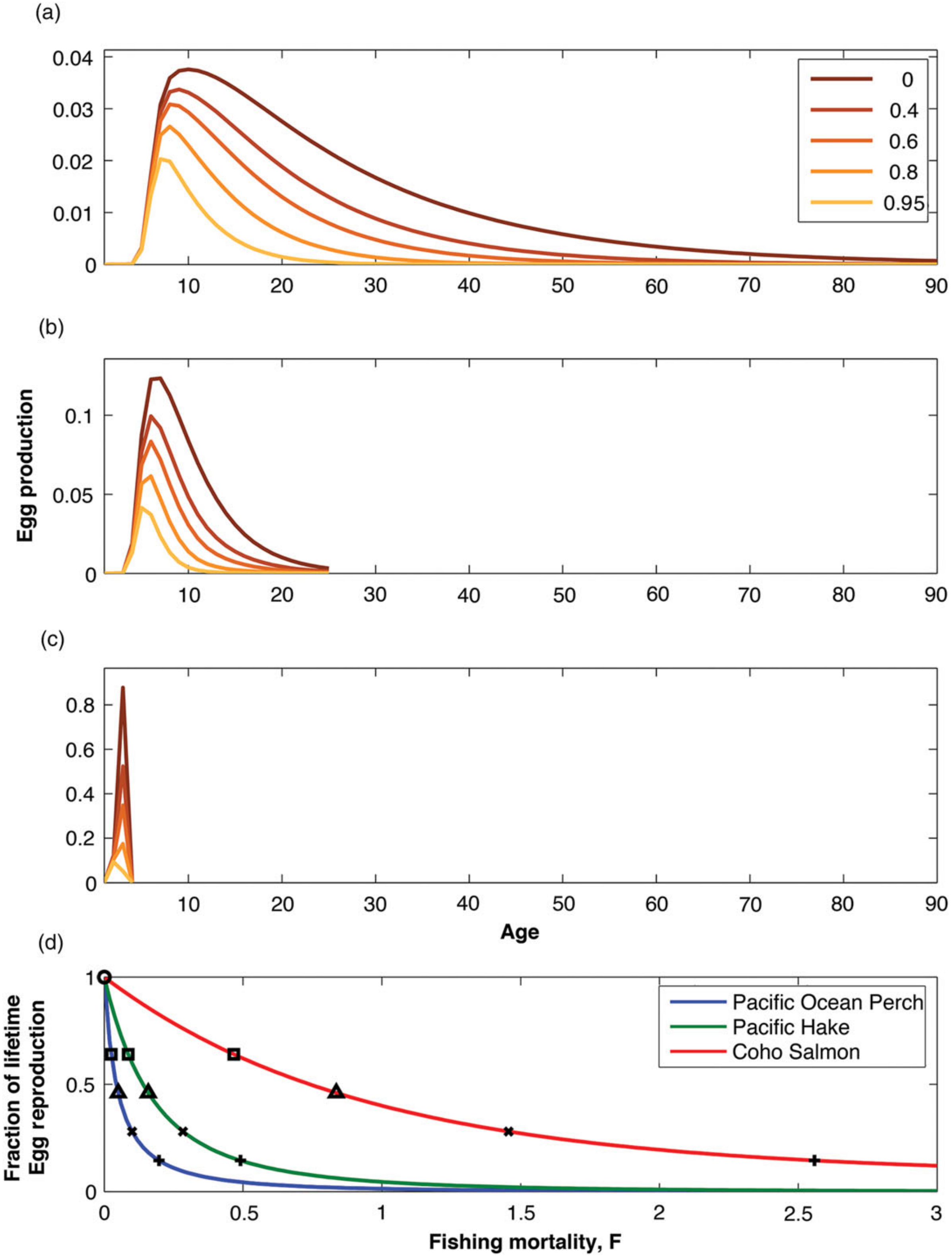

Figure 3. The probability distributions of egg production over age with no fishing for (a) POP, (b) Pacific Hake, and (c) coho salmon along the west coast of the United States, and the diminished distributions at four different levels of fishing. Each is identified by their Exploitation Index, EI ($\mathrm{EI} = (1-\mathrm{FLEP})/(1-\mathrm{FLEP}_C)$), where FLEP is the fraction of unfished lifetime reproduction (thus lower EI = lower fishing), and FLEP_C is the value at which equilibrium recruitment collapses to zero, here assumed to be 0.1 for all three species for the ease of comparison of the effects of age structure. (d) The different values of fishing mortality rate and FLEP that produces the five values of EI for each species in (a)–(c) with the circle indicating EI = 0, the squares indicating EI = 0.4, the triangles indicating EI = 0.6, the *x*'s indicating EI = 0.8, and the +'s indicating EI = 0.95. The value of EI declines from 1.0 to 0.0 as fishing increases from no fishing to the point at which the population would collapse (i.e. FLEP = 0.1).

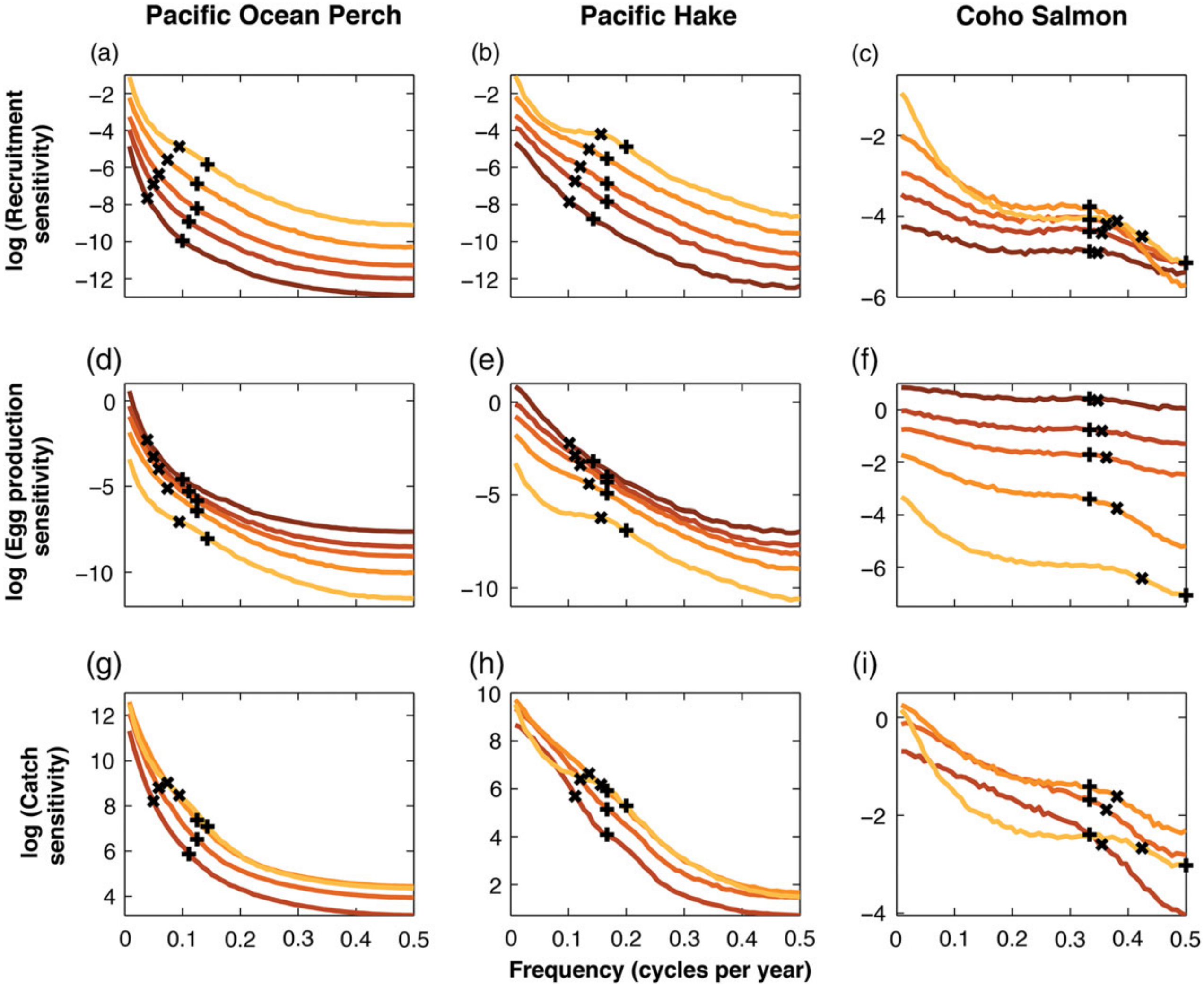

Figure 4. Sensitivities of species and variables to the frequencies of variability in the environmental variable affecting survival. The sensitivity is the ratio of the variance in the variable about its equilibrium value to the variance in the variable that is being forced by the environment (here recruitment survival), about its mean. The sensitivity of recruitment expected from the egg – recruit relationship (a – c, i.e. the green line in Figure 2), egg production (d – f, i.e. the purple signal in Figure 2), and catch (g – i) in POP (a, d, and g), Pacific hake (b, e, and h), and coho salmon (c, f, and i) to frequencies of environmental variability at different levels of fishing are indicated the same as in Figure 3. The *x*'s indicate the inverses of the means and the +'s indicate the inverses of the modes of the spawning age distributions in Figure 3.

These patterns of sensitivity to different frequencies illustrate the differences in the characteristics of cohort resonance among species with different longevities, and how they change with fishing. The primary feature in these is greater sensitivity to frequencies near the inverse of the means (*x*'s) and modes (+'s) of the spawning age distributions in Figure 3 (Bjørnstad *et al*., 2004; Worden *et al*., 2010), which is most obvious in the recruitment signal that results from the egg–recruit relationship (Figure 4a–c). These peaks are stronger in shorter-lived species (e.g. hake and coho salmon), and become stronger with greater fishing (Worden *et al*., 2010). Note that the magnitudes of the sensitivity of recruitment over all frequencies actually increase with fishing. That effect is subsequently occluded by the added large random variability, hence it is not present in the spectra of annual egg production (Figure 4d–f) and catch (Figure 4g–i). These latter variables are relatively more responsive to low frequencies, even in the unfished case. This is because these two variables are sums over multiple cohorts, hence over multiple past values of random recruitment, which has the effect of smoothing out the high frequencies in environmental variability seen in recruitment. However, they also show a small effect of the resonant peak at generational time-scales in salmon, and in the heavily fished case for Pacific hake. The order of the sensitivities in catch signals at different levels of fishing is not the same as the order in egg production because equilibrium catch first increases, then decreases as fishing increases.

The important characteristic of cohort resonance here in the context of Hjort (1914) is that the fluctuations in recruitment to a population do not simply follow the variability in survival through the recruitment stage, as would occur if egg production was relatively constant as commonly assumed [and was posited by Hjort (1914)]. Rather, as explained in Figure 2, variable recruitment survival multiplies the result of *variable* egg production, which varies due to the effects of past recruitment. That effect is demonstrated in Figure 5, where the expected recruitment signal from the egg–recruit relationship is relatively constant in the unfished case, but as fishing increases, it becomes a lagged, smoothed version of past recruitment, with increasing resemblance to past

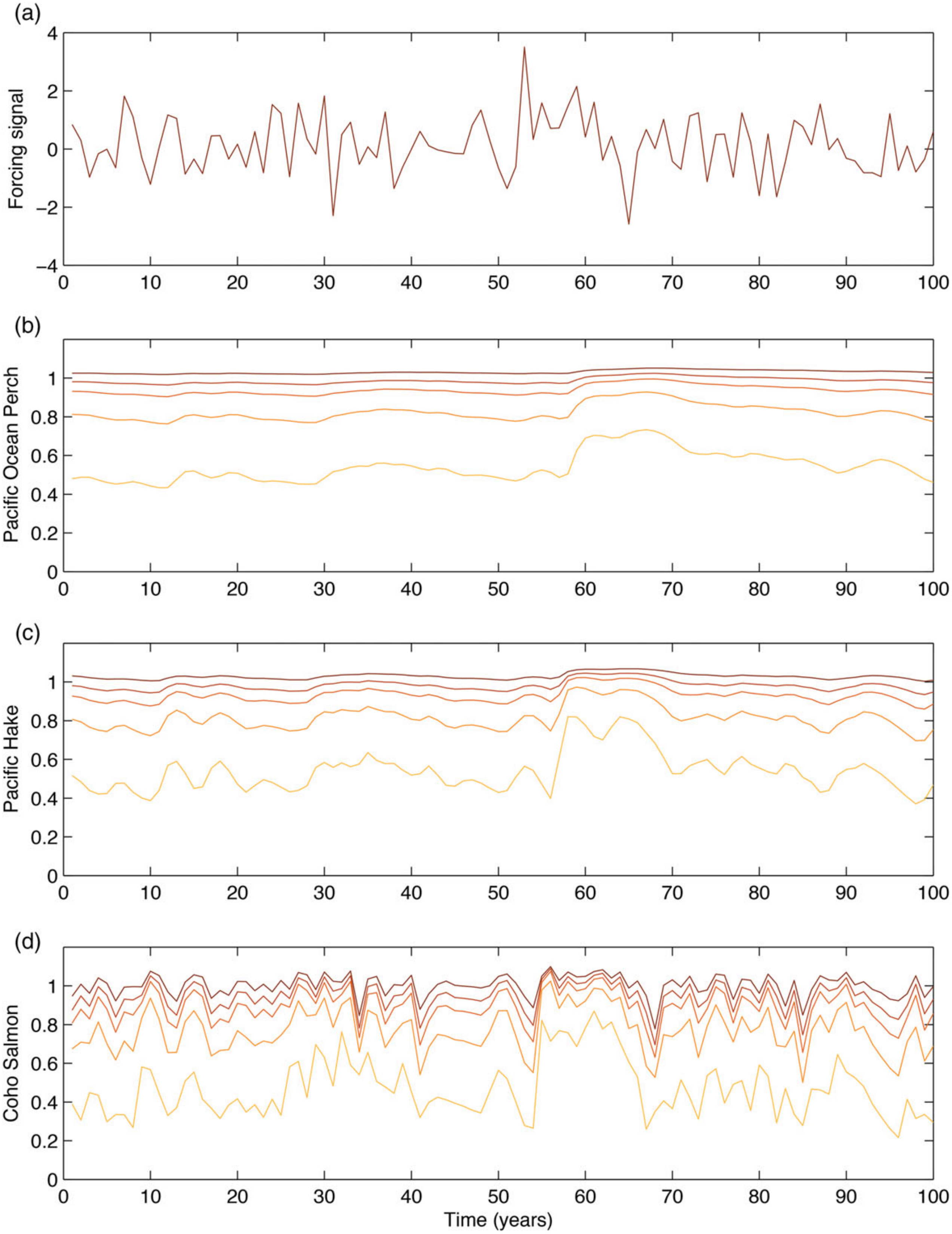

Figure 5. The effects of past recruitment on current recruitment through variability in egg production. The recruitment signal we can observe empirically is the product of current random recruitment survival (a) and current expected recruitment from the egg – recruit relationship (i.e. the green signals in Figure 2) for POP (b), for Pacific Hake (c), and for coho salmon (d), which all depend on the effects of past recruitment through current egg production. The different values of the exploitation index are indicated in (b), (c), and (d) in the same way as in Figures 3 and 4.

recruitment as the cohort resonance effect becomes stronger. For example, the dip in recruitment survival at year 51 becomes a dip in expected recruitment near year 58 for POP (a lag of 7 years), a similar dip in expected recruitment near year 56 for Pacific hake (a lag of 5 years), and a dip during years 53 and 54 (a lag of 2–3 years) for coho salmon. These are important because they serve to reinforce temporal variability in the environment on generational time-scales (see explanation of lower part of Figure 2). It must be emphasized that fishery biologists [e.g. Hjort (1914) and others] could not have seen the signals in Figure 5 because actual sampling of recruitment occurs after the addition of variability in survival (i.e. the red signal in Figure 1), which occludes the signal seen in Figure 5.

Empirical observations of an increase in variability with fishing have been made in terms of variables such as egg production (Hsieh *et al.*, 2006) and catch (Bjørnstad *et al.*, 2004). Here, we show how the coefficient of variation (*CV*s) of recruitment measured at two points in the life history, and the *CV*s of egg production and catch change with fishing (Figure 6). These plots of the *CV*s arising from environmental variability that is white noise in recruitment survival show how the relative amount of variability in various quantities in fish populations would increase with fishing (Figure 6a–d). Unfished variability in the recruitment resulting from the egg–recruit relationship (Figure 6a, the green signals in Figure 2, and the time-series shown in Figure 5b–d) is greatest in the shortest lived species, but increases more rapidly in the longer lived. Unfished variability in observed recruitment (Figure 6b, the red signals in Figure 2) is quite similar for the three species because they are dominated by the same multiplicative lognormal white variability in survival. There is little increase in observed recruitment variability with fishing, except near collapse (Figure 6b). This lack of an observable increase is also due to recruitment observations being made just after the introduction of environmental variability experienced during the larval stage. Any increase in variability of this relatively small signal from the egg–recruit relationship is occluded by the large, constant magnitude of the environmental noise, until just before collapse. With no fishing, the *CV*s of both egg production (Figure 6c) and catch (Figure 6d) are less than those of observed recruitment (Figure 6b), because they are sums over current age classes, thus weighted sums over past random recruitments. This smoothing effect is greater for longer-lived species because they sum over the results of a greater number of past random recruitments. However, importantly, as fishing increases, the *CV* of egg production increases more rapidly in the longer-lived species as seen in Figure 6a. This difference is due primarily to age truncation reducing the number of past random recruitments influencing egg production each year, thus reducing the smoothing of variable recruitment (Figure 2). The *CV* of catch varies slightly differently because equilibrium catch at first increases then declines as fishing increases. However, similar to the *CV* of egg production, the *CV* of catch increases more steeply with fishing in the longer-lived POP than in salmon and hake.

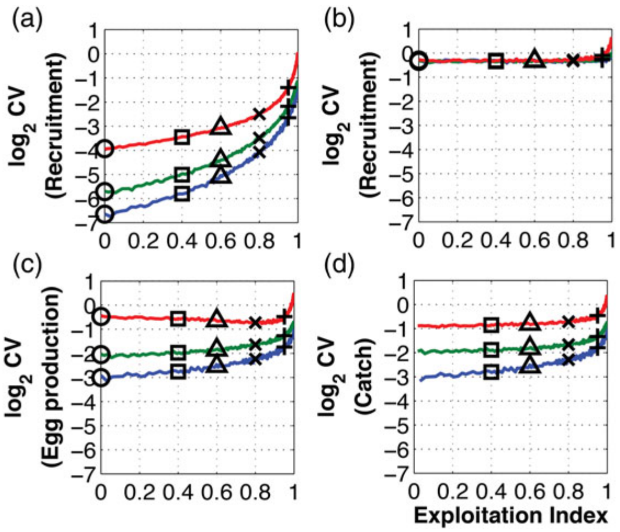

Figure 6. The effects of different levels of fishing on the variability (coefficient of variation) in recruitment expected from the egg–recruit relationship (a, the green signals in Figure 2), the recruitment after variability is added (b, the red signals in Figure 2), egg production (c, the purple signals in Figure 2), and catch (d) depend on fishing as it varies from no fishing (EI = 0) to the collapse point (EI = 1.0) for coho salmon (light grey line, or red line online), Pacific hake (dark grey line, or green line online), and POP (black line, or blue line online). The symbols indicate the same values of FLEP as in Figure 3. Note that the logarithms here are to the base 2 to allow easy comparison of doubling.

The empirical spectra of each these species (Figure 7) are consistent with these findings regarding the order of magnitudes of expected responses, but they require care in interpretation (Greenman and Benton, 2005). The observed signals are the product of the frequency selective sensitivity of each species and the frequency content of the actual environment over the past several decades, so would not necessarily be expected to match the frequency selectivity exactly. However, we can expect from Figures 4 and 6 that of these three species, coho salmon would be the most likely to exhibit peaks on generational time-scales, and they would be near period 3 (Figure 4). Therefore, the spectrum of spawning abundance for Oregon Coast Natural coho salmon (Rupp *et al.*, 2012) displayed significant variability in spawning abundance near period 3 from 1980 through the mid-1990s. It also has substantial variability on time-scales near 20 years, but that is not identified as significant by the wavelet analysis, and is outside the cone of significance due to series length. The *CV* of this spawner abundance time-series is 0.41. The spawning-stock biomass of Pacific hake displays substantial variability between 8 and 16 years from the late 1970s through the end of the series, but most of this is outside the cone of significance due to the series' length. The *CV* for this time-series is 0.31. The spawning-stock biomass for POP shows greater variance near a period of 10 years throughout the series from the 1970s to the year 2000, with a *CV* of 0.31 also.

Discussion

Cohort resonance is a recently discovered mechanism that contributes substantially to variability in fluctuating fish populations. It is an interaction between the fluctuating age structure of a fish population and the density-dependence in the early lives of fish. The life history of a species determines its response to environmental variability in early life, notably with greater sensitivity to specific frequencies. Cohort resonance is named for the *resonance* mechanism underlying the inherent sensitivity of age-structured populations to generational frequencies, i.e. it consists of noise exciting a natural frequency of a system. The mechanism underlying sensitivity to low frequencies is different, having more to do with the wandering behaviour of linear populations with weak density-dependence.

Species differences

A key feature of cohort resonance illustrated here is that its relative effect on a species depends critically on the species longevity.

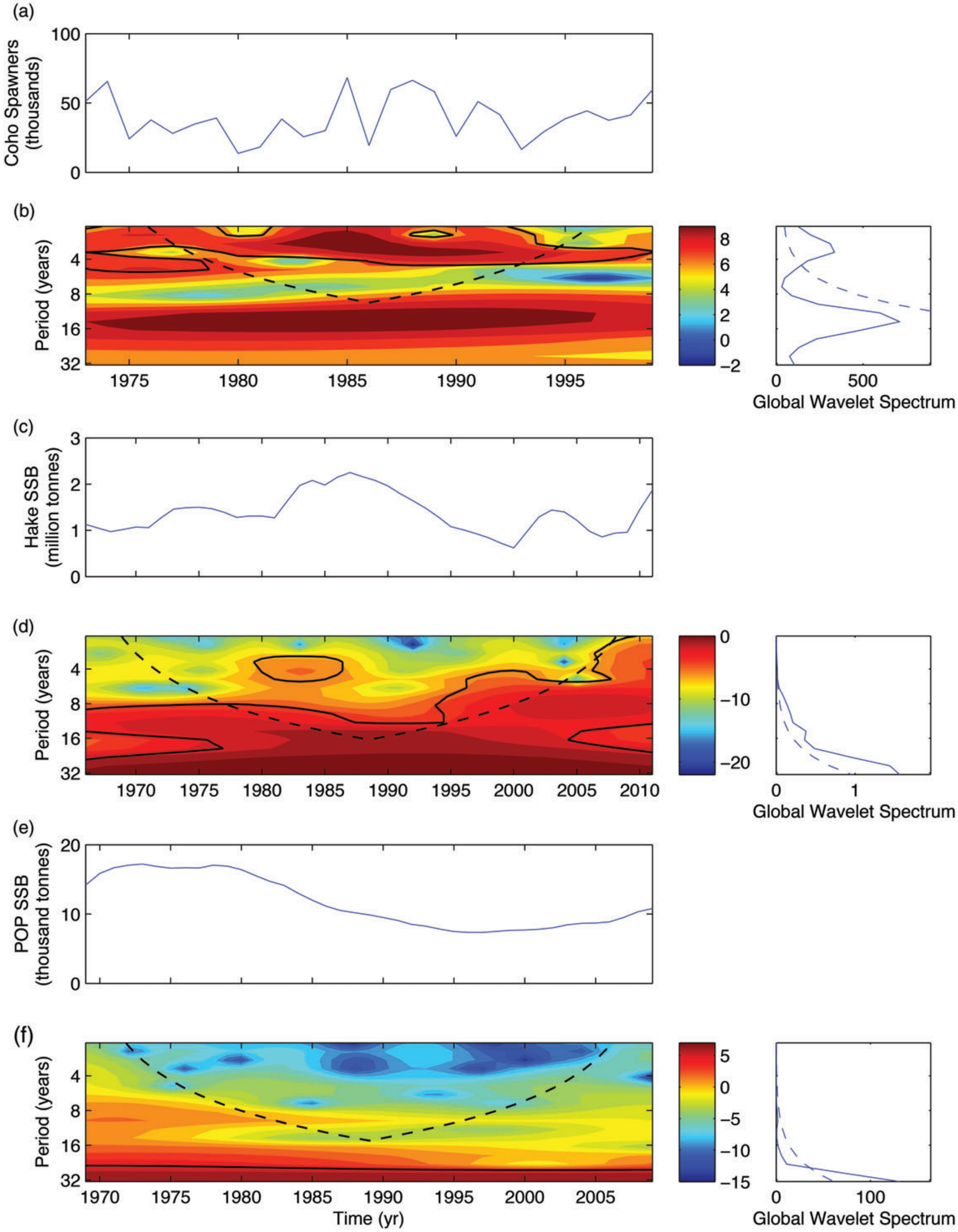

Figure 7. Spectra of the species analysed. Time-series (a, c, and e) and wavelet spectra (b, d, and f) for coho salmon, Pacific hake, and POP. In the wavelet spectra, the dashed lines indicate the "cone of significance" due to limited series length, i.e. only results at periods less than the period indicated are significant (Torrence and Compo, 1998). Bold lines indicate significance by a different criterion, whether they are significantly different from an AR2 process with the same intra-series correlation. The colour bars indicate the logarithms to the base 2 of the variance density. The Global Wavelet Spectra each represent the wavelet spectrum of each complete series.

Shorter-lived fish are much more sensitive to environmental variability than longer-lived species. Here unfished coho salmon, which live 3 years, were approximately six times as variable as unfished POP (∼90 years), and unfished Pacific hake (∼25 years) were twice as variable (Figure 6c, where actual exact values at $\mathrm{EI} = 0$ are 0.126:0.235:0.712).

Increased variability with fishing

A second key feature of cohort resonance illustrated here is that variability in several population variables increases with fishing at rates that depend on longevity. While without fishing, coho salmon egg production and catch were more sensitive to environmental variability than the other two species, as fishing increased, the sensitivities to environmental variability of the longer-lived species (hake and POP) increased more rapidly than in coho salmon, so that under heavy fishing (i.e. $\mathrm{EI} = 0.95$), the environmental sensitivity of egg production in the longest lived species was about half that of the shortest lived. Associated with these increases in overall sensitivity to the environment was a frequency selective increase in sensitivity to slow changes in the environment and variability on generational time-scales (Figure 4).

The predominant proposed explanations of increasing variability with fishing have involved unstable behaviour of over-compensatory models (Anderson *et al.*, 2008; Shelton and Mangel, 2011a), and while details are the subject of ongoing debate (Shelton and Mangel, 2011a; Sugihara *et al.*, 2011), these authors agree that unstable models are a key to their explanations. Both of these models depend on the well-known ability of population models with over-compensatory density-dependence in the egg-to-recruit relationship with display highly variable, possibly chaotic behaviour (Hassel *et al.*, 1976; Botsford, 1992), which cohort resonance does not. In most fish populations, it is difficult to determine whether the egg–recruit relationship is truly over-compensatory (Dorn, 2002; Zhou, 2007). Yet most fish populations show the compensatory decline in slope as abundance increases from very low values, which is the form driving the cohort resonance effect.

If cohort resonance is the dynamic mechanism responsible for increasing variability with fishing, the analyses here would shed light on the roles of various proposed biological factors. For example, age truncation is certainly a central factor in cohort resonance (Figure 3), but maternal effects would not be necessary for variability to increase with fishing. Also, selection for changes in life history parameters could exacerbate variability, but again, they would not be necessary.

Empirical observations

Future usefulness and understanding of cohort resonance will depend on identification of empirical examples. One example is the recent demonstration that an extreme form of cohort resonance explains the "cohort dominant" cycles in sockeye salmon (i.e. cycles consisting of a single spawning run of high abundance followed by several smaller runs, Ricker, 1997; Myers *et al.*, 1998; White *et al.*, 2014). The conditions that would allow the cohort resonance effect to cause decades of cycles similar to the cohort dominant cycles in sockeye salmon were: narrowness of the spawning age distribution, low persistence with regard to the stock–recruit relationship, and high variability in juvenile survival (White *et al.*, 2014). More important to us here perhaps, this investigation also led to the realization of a somewhat unique characteristic of cohort resonance: since it arises from environmental forcing of a *stable* population, a population may satisfy the conditions for cohort resonance, yet not actually display the characteristic behaviour of cohort resonance simply because it has not recently been excited by an appropriate environmental signal. This is contrary to the expectations when analysing population data to evaluate the presence of cycles due to a mechanism involving actual instability.

Another empirical example is the recent investigation by Rouyer *et al.* (2012) of the effects of fishing on the spectra of population variability in 24 North Atlantic fish stocks, including the herring and cod stocks in Hjort (1914). The slope of the variance spectrum was shown to be shallower (i.e. include more high frequencies) in stocks for which the mean age had declined, consistent with expectations from cohort resonance.

The three species examined here are further examples of empirical observations of cohort resonance. Because the frequency-dependent filtering is only part of what produces these observed signals, they would not be expected to be exactly the same as the theoretical projections. The *CVs* of the empirical egg production time-series for coho salmon, Pacific hake, and POP in Figure 7 were 0.41, 0.31, and 0.31, respectively, or ratios of 1.0:0.76:0.76, when compared with the predicted values at $\mathrm{EI} = 0.8$ in Figure 6c of ∼1.0:0.5:0.3. The spectra showed high variance near the generational frequency for the species for which it was expected to be strongest, coho salmon, and in general, the rates of decline of variance with frequency in the global wavelet spectra (Figure 7b–f) loosely followed those expected from Figure 4.

Analysis of these time-series illustrates some of the challenges in detecting the spectral sensitivities in cohort resonance. One is that long time-series are necessary, especially for long-lived species. In our wavelet analyses (Figure 7), we have shown periods out to 32 years to illustrate the presence of variance at low frequencies, but even periods >8 years for salmon and 16 years for the other two species lie outside the cone of significance. Longer time-series will be necessary to detect such long periods. A second challenge is that much of the available data may only be the results from fitting stock assessment models. The frequency content would be influenced by the model used in the fitting. In Figure 7, this was the case for Pacific hake and POP, which are taken from stock assessments, but could not affect coho salmon, for which abundances are direct observations rather than model products. A third challenge in detecting cohort resonance effects is the previously mentioned fact that population time-series depend on environmental variability in the recent past, as well as the population sensitivity we are trying to detect.

It is interesting that empirical evidence of the effects of cohort resonance was not detected by Hjort (1914), nor anyone else, during the 90 years from 1914 to 2004. This is likely due to two reasons: (i) detection from early life history data would have involved examining recruitment, which is dominated by environmental noise that would overwhelm any cohort resonant variability from the egg to recruit relationship (Figure 6b when compared with Figure 6a) and (ii) most results in 1914 were presumably based on relatively lightly fished, reasonably long-lived species, in which cohort resonant effects are weaker. For example, Hjort (1914) was mainly concerned with herring and cod off the coast of Norway, which had lifespans near 10 years.

Although cohort resonance would have been difficult to detect empirically, one might further ask why the cohort resonance phenomenon was not discovered earlier by those working in population dynamics? The answer is, at least in part, because cohort resonance occurs in stable populations. Mathematical ecologists working in population dynamics tend to look for instabilities when trying to answer questions regarding large fluctuations. An example of locally unstable cycles in fisheries due to over-compensatory density-dependence in stock recruitment is the cyclic variability of period $2T$ in some marine populations (e.g. Ricker, 1954; Botsford and Wickham, 1978).

Mechanisms that are similar to, or are a part of, cohort resonance have been identified empirically in previous quantitative analyses. For example, a meta-analysis of variability in early survival of fish indicated greater variability in populations fished to low abundance, and suggested that the mechanism was stochastic density-independent mortality in the egg and larval stages, followed by compensatory (not over-compensatory) density-dependent mortality in the juvenile stage (Myers, 2001; Minto *et al.*, 2008).

Theoretical considerations

The theoretical basis for cohort resonance ties it to a broad range of other topics in population dynamics. The analysis demonstrating cohort resonance employs a model of how the population varies with respect to its equilibrium value (e.g. Worden *et al.*, 2010). This model has essentially the same form as a Leslie matrix, which means that its dominant behaviour is geometric growth, which in the stable case, would return the abundance to equilibrium. It also means that the next largest mode of behaviour is a cyclic approach to equilibrium, mathematically the same cyclic transients one sees when a simulation of a Leslie matrix starts from an arbitrary initial age structure (Sykes, 1969). These are essentially the same kind of transients one could see when a population is placed under the protection of a marine protected area (White *et al.*, 2013). This also means that one can glean information regarding which life history characteristics will lead to greater propensity for cycling at period T from studies of that same topic for other species (e.g. Taylor, 1979, for insects).

Another valuable link to theory is the fact that the increase in variance and change in frequency response with fishing due to cohort resonance are similar to the increases in variance and autocorrelation being investigated as Early Warning Signs (EWS) of deleterious changes in ecosystem state. The increase in variance due to cohort resonance near the population collapse point is illustrated in Figure 6, and the increase in autocorrelation follows from the increasing sensitivity to low frequencies with fishing in Figure 4. In more general settings, the role of increasing variance and autocorrelation as leading indicators of tipping points or regime shifts has been a subject of great recent interest (Scheffer *et al.*, 2009, 2012; Boettiger *et al.*, 2013). In the population models of the cohort resonance effect, we do not have a saddle–node bifurcation, which is commonly the focus in EWS research, but instead, we have what is known as an exchange of stability. Cohort resonance is quite similar to the experimental system examined by Drake and Griffen (2010) who analysed the response of a laboratory population of Daphnia to reduced food levels for signs of increased variance in the abundance time-series before extinction. What is different and interesting about cohort resonance is the role played by age structure in generating the increased variance in a system where stochasticity is important. The recent finding that an increase in catch variability preceded collapses in North Pacific crab fisheries is a suggestion that cohort resonance may have been involved (Litzow *et al.*, 2013). Much work remains in relating our results to the growing EWS literature and developing rigorous approaches to using these signals to forecast shifts (Boettiger and Hastings, 2012).

Climate change

The existence of cohort resonance in age-structured fish populations has important implications for the effects of climate change on marine ecosystems (Botsford *et al.*, 2012). It provides information regarding the effects of possible changes in the frequency content of environmental signals (e.g. changes in the frequency of El Niños). Such changes in El Niños have been observed empirically in the past (Cobb *et al.*, 2003) and are also predicted by global climate models in the future (Timmermann *et al.*, 1999). A second implication for climate change is identification of the confounding of potential slow changes in abundance due to fishing or climate change, with increasing sensitivity to low frequencies due to cohort resonance [the "cloaking" effect of Bjørnstad *et al.* (2004)].

In summary, the phenomenon of cohort resonance seems to be a valuable addition to the search for greater understanding of fluctuations in fished populations which Hjort initiated 100 years ago. Further analyses and continued comparison with empirical data will likely produce results that could be useful in fisheries management and anticipating the effects of climate change. Additional work is needed to compare the expectations of cohort resonance to empirical data.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

This research is part of US GLOBEC synthesis activities, and was supported by National Science Foundation grant NSF OCE0815293. We thank Will White, Jason Whittington, and two reviewers for helpful comments.

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Handling editor: Manuel Hidalgo

ICES Journal of Marine Science

ICES Journal of Marine Science (2014), 71(8), 2171–2185. doi:10.1093/icesjms/fst200

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food for thought

BOFFFFs: on the importance of conserving old-growth age structure in fishery populations

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Hixon, M. A., Johnson, D. W., and Sogard, S. M. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. – ICES Journal of Marine Science, 71: 2171–2185.

Received 17 July 2013; accepted 26 October 2013; advance access publication 29 December 2013.

The value of big old fat fecund female fish (BOFFFFs) in fostering stock productivity and stability has long been underappreciated by conventional fisheries science and management, although Hjort (1914) indirectly alluded to the importance of maternal effects. Compared with smaller mature females, BOFFFFs in a broad variety of marine and freshwater teleosts produce far more and often larger eggs that may develop into larvae that grow faster and withstand starvation better. As (if not more) importantly, BOFFFFs in batch-spawning species tend to have earlier and longer spawning seasons and may spawn in different locations than smaller females. Such features indicate that BOFFFFs are major agents of bet-hedging strategies that help to ensure individual reproductive success in environments that vary tremendously in time and space. Even if all else were equal, BOFFFFs can outlive periods that are unfavourable for successful reproduction and be ready to spawn profusely and enhance recruitment when favourable conditions return (the storage effect). Fishing differentially removes BOFFFFs, typically resulting in severe truncation of the size and age structure of the population. In the worst cases, fishing mortality acts as a powerful selective agent that inhibits reversal of size and age truncation, even if fishing intensity is later reduced. Age truncation is now known to destabilize fished populations, increasing their susceptibility to collapse. Although some fisheries models are beginning to incorporate maternal and other old-growth effects, most continue to treat all spawning-stock biomass as identical: many small young females are assumed to contribute the same to stock productivity as an equivalent mass of BOFFFFs. A growing body of knowledge dictates that fisheries productivity and stability would be enhanced if management conserved old-growth age structure in fished stocks, be it by limiting exploitation rates, by implementing slot limits, or by establishing marine reserves, which are now known to seed surrounding fished areas via larval dispersal. Networks of marine reserves are likely to be the most effective means of ensuring that pockets of old-growth age structure survive throughout the geographic range of demersal species.

Keywords: age truncation, big old fat fecund female fish (BOFFFF), egg/offspring size/quality, maternal effects, recruitment, relative fecundity, stock productivity/stability, storage effect.

> Logic surely demands that a fishery for a species having intermittent recruitment must somehow eschew the common practice of truncating the age structure.—Alan Longhurst (2002, p. 6)

Despite many models, truly understanding the mechanisms underlying the dynamics of exploited fish stocks remains elusive. Hjort (1914) was clearly prescient in his key assumption that the population dynamics of marine teleost fish are driven largely by variation in larval survival. His two major hypotheses to explain variable larval mortality focused on, first, larvae finding sufficient food or not, and second, larvae drifting to or from suitable habitat (Hjort, 1926). Although it is clear that mortality during the larval phase is indeed the major source of density-independent mortality in marine fish (Houde, 1987), it has also been lamented that fisheries science has spent far too much time narrowly focused on these two particular hypotheses (Houde, 2008).

We believe that there are implications of Hjort's work that have not been fully embraced by fisheries science. In the chapter entitled "Fluctuations in Quality" of his classic treatise, Hjort (1914) explored variation in the condition of the parental stock, noting that large Atlantic cod (*Gadus morhua*) contain disproportionately more fat that smaller fish. In doing so, Hjort initiated the first excursion into what would eventually be called "maternal effects", the influence of the maternal phenotype on the phenotype of her offspring (Mousseau and Fox, 1998). Here, we expand this definition to include the effects of female age and size on the timing and location of spawning, which are also likely to affect offspring growth and survival. It is now known that maternal effects are evident in a broad diversity of fish and other organisms (reviews by Green, 2008; Marshall *et al.*, 2008). However, fisheries models have historically assumed that many small, young, mature females are reproductively equivalent to fewer large, old females of the same total mass.

In this essay, we summarize the variety of ways that big old fat fecund female fish (hereafter, "BOFFFFs", Figure 1) contribute substantially to stock productivity and stability in ways considerably different from smaller females—i.e. all spawning-stock biomass (SSB) is not the same after all. Calling attention to the value of BOFFFFs matters because fisheries disproportionately remove BOFFFFs and typically truncate age and size distributions, leaving only younger, smaller spawners (Trippel, 1995; Levin *et al.*, 2006; Sharpe and Hendry, 2009; Fisher *et al.*, 2010; Stewart, 2011). Severe age truncation may thus lead to "longevity overfishing" (Beamish *et al.*, 2006). Therefore, management is likely to enhance fisheries by conserving old-growth age structure and ensuring survival of a broad range of adult ages and sizes. Although such protection has only rarely been implemented in fisheries management, this thesis is not new and is shared by many (e.g. Longhurst, 2002; Francis, 2003; Berkeley *et al.*, 2004a; Froese, 2004; Birkeland and Dayton, 2005; Berkeley, 2006; Hsieh *et al.*, 2006, 2010; Francis *et al.*, 2007; Froese *et al.*, 2008; Rouyer *et al.*, 2011, 2012).

Herein, we review the biological traits that vary with fish size and/or age and the implications of these traits for population resilience. We do not explicitly consider the economic benefits or costs of management strategies that preserve BOFFFFs. For many fisheries, larger individuals are more valuable economically and there are potential financial trade-offs between harvesting these fish vs. implementing management measures to protect them. Mullon *et al.* (2012) address these trade-offs in a modelling framework comparing harvest scenarios with either a minimum size or a maximum size and varying size-based price differentials. They note that in some cases the two scenarios result in comparable economic gains but disparate success in matching conservation objectives. Our focus here is on the long-term biological goal of maintaining population stability.

Figure 1. A big (1.1 m), old (ca.100 years), fat (27.2 kg), fecund female fish, in this case a shortraker rockfish (*Sebastes borealis*) taken off Alaska (Karna McKinney, Alaska Fisheries Science Center, NOAA Fisheries Service).

We first summarize the reproductive biology of large old female fish, showing that BOFFFFs not only produce far more eggs than smaller females, even after accounting for body size, but also often produce larger or better provisioned eggs and larvae that grow faster and are better capable of withstanding starvation. Additionally, by spawning at different times or in different locations than smaller females, BOFFFFs extend the likelihood that at least some of a population's larvae will encounter favourable environments (a by-product of selection for individuals to maximize reproductive success). That is, the BOFFFFs that are characteristic of old-growth age structure contribute substantially to stock productivity. We then briefly review the fact that fishing typically causes extreme size and age truncation, i.e. severe declines in the abundance of BOFFFFs. Fishing thereby often becomes an agent of artificial selection causing both phenotypic and genetic shifts in fished populations in ways that not only inhibit fisheries productivity and stability, but also are difficult to reverse. In fact, size and age truncation destabilizes fish population dynamics, which renders fisheries less predictable and more subject to collapse. We conclude with a brief review of the policies by which BOFFFFs can be better conserved by fisheries management and explore why, despite Hjort's (1914) early explorations of parental effects, maintaining old-growth age structure by conserving BOFFFFs is still—a full century later—not yet standard practice.

Relative fecundity of BOFFFFs

Fecundity generally increases with female age simply as a function of body size because a larger body cavity allows development of larger ovaries. In fisheries applications, the increase in fecundity with body size is accounted for by using the metric of SSB, which is an estimate of the total weight of mature fish in the population. Application of SSB in assessment models relies on the assumption that females of different sizes produce the same number and quality of offspring per unit of body weight. Here, we do not consider the increase in fecundity with body size to be a maternal effect unless there is a difference in weight-specific or relative fecundity, the number of eggs per gramme of female body weight. If relative fecundity differs with maternal traits, then SSB is not an adequate metric for the reproductive potential of populations with different maternal age/size compositions. Cooper *et al.* (2013) provide a clear example of the contrast between SSB and total egg production (TEP) with increasing age truncation (Figure 2).

Especially in long-lived species with low natural mortality, females devote increasingly more energy into reproduction than growth as they age (review by Roff, 1992). In fact, relative fecundity has been found to increase with maternal age or size in a wide range of species (Table 1). Stock assessments are increasingly incorporating such size- and age-dependent effects on fecundity. The degree to which older females produce disproportionate numbers of larvae varies greatly among species. In a review of 41 species of rockfish (genus *Sebastes*), Dick (2009) found that some of these differences could be explained by phylogeny. For example, species in the

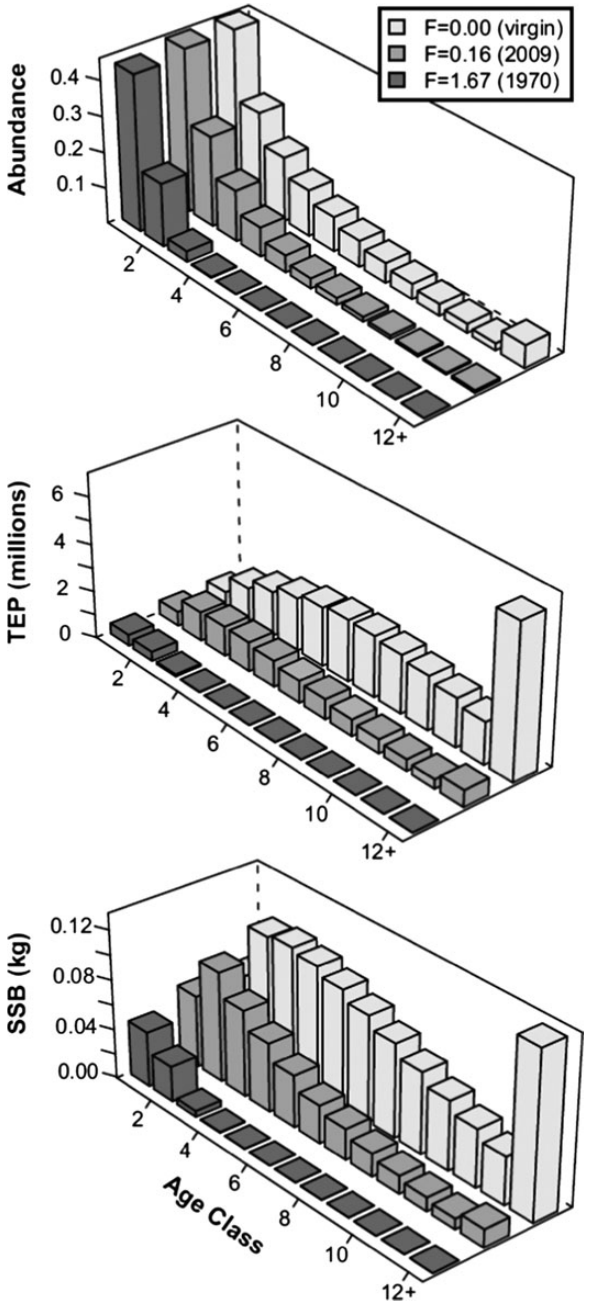

Figure 2. Modelled abundance, TEP, and SSB at three fishing mortality rates (*F*) per recruit of spotted seatrout (*Cynoscion nebulosus*). Note the extreme age truncation and decline in egg production caused by even moderate fishing (Cooper *et al.*, 2013).

Table 1. Representative teleost species with relative (weight-specific) fecundity documented to increase with female age and/or size.

Species	Reference
Clupea harengus	Oskarsson and Taggart (2006)
Clupea pallasi	Hay (1985)
Coregonus pidschian	Dupuis and Sutton (2011)
Coregonus clupeaformis	Johnston *et al.* (2012)
Dicentrarchus labrax	Mayer *et al.* (1990)
Gadus morhua	Marteinsdottir and Begg (2002)
Melanogrammus aeglefinus	Hislop (1988)
Merluccius merluccius	Mehault *et al.* (2010)
Sebastes alutus	Haldorson and Love (1991)
Sebastes brevispinis	Stanley and Kronlund (2005)
Sebastes caurinus	Dick (2009)
Sebastes chlorostictus	Haldorson and Love (1991)
Sebastes crameri	Dick (2009)
Sebastes dalli	Haldorson and Love (1991)
Sebastes diploproa	Dick (2009)
Sebastes elongatus	Haldorson and Love (1991)
Sebastes entomelas	Boehlert *et al.* (1982), Stafford (2012)
Sebastes flavidus	Sogard *et al.* (2008), Stafford (2012)
Sebastes goodei	Stafford (2012)
Sebastes melanops	Bobko and Berkeley (2004)
Sebastes melanostomus	Beyer *et al.* (in press)
Sebastes miniatus	Haldorson and Love (1991)
Sebastes mystinus	Sogard *et al.* (2008)
Sebastes ovalis	Beyer *et al.* (in press)
Sebastes paucispinis	Haldorson and Love (1991)
Sebastes rosaceus	Haldorson and Love (1991)
Sebastes rosenblatti	Haldorson and Love (1991)
Sebastes rufus	Haldorson and Love (1991)
Sebastes saxicola	Haldorson and Love (1991)
Sebastes semicinctus	Haldorson and Love (1991)
Sebastes serranoides	Haldorson and Love (1991)
Seriphus politus	DeMartini (1991)
Tilapia zillii	Coward and Bromage (1999)

subgenus *Acutomentum* showed limited evidence of size-related differences in relative fecundity. In contrast, species in the subgenera *Rosicola* and *Sebastomus* demonstrated strong increasing trends with female size.

For multiple-batch spawners (fish that spawn multiple times in a season), total annual egg production will of course depend on the number and size of batches released each season. In fisheries applications, the common assumption is that batch number does not vary with female size or age. A thorough review by Fitzhugh *et al.* (2012) reported 21 species in which the number of batches increases with female age or size, four species that show a decrease, and nine species with no differences. Based on modelling studies of different hake (*Merluccius*) species, Field *et al.* (2008) estimated a dramatic increase in batch number with age, from one batch per year at age 2 to fourteen batches per year at age 15. As with other aspects of maternal influences on reproduction, there is a clear trend towards BOFFFFs contributing disproportionately to future cohorts, but sufficient variability to indicate that such reproductive parameters must be evaluated on a species-by-species basis. Such interspecific variability adds further complexity to the development of management approaches that incorporate maternal effects.

In addition to exhibiting lower relative fecundity, younger, smaller females have been observed to skip spawning altogether in some years. Evidence of this effect has been observed in Atlantic cod (Rideout and Rose, 2006), and the rockfish *Sebastes alutus* (Hannah and Parker, 2007) and *S. aurora* (Thompson and Hannah, 2010). Rideout *et al.* (2006) demonstrated a clear relationship of reduced energy stores in the liver associated with skipped spawning, harkening back to Hjort's (1914) prescient analysis of cod. Variation in the extent of skipped spawning among years may also be associated with differences in the quality of the larval environment (Rideout *et al.*, 2006; Hannah and Parker, 2007).

Maternal effects on offspring size and quality

Intraspecific variability in offspring size or offspring quality has been widely observed in fish (Bagenal, 1971; Bernardo, 1996).

Table 2. Representative teleost species with offspring size and/or quality documented to increase with female age and/or size.

Species	Offspring trait	Maternal trait	Reference
Clupea harengus	Egg size	Length	Blaxter and Hempel (1963)
Clupea pallasi	Egg size	Length	Hay (1985)
Coregonus clupeaformis	Egg size	Age	Johnston *et al.* (2012)
Cyprinus carpio	Egg size	Age	Weber and Brown (2012)
Engraulis anchoita	Egg size	Length	de Ciechomski (1966)
Gadus morhua	Egg size	Length and age	Kjesbu (1989), Chambers and Waiwood (1996), Marteinsdottir and Steinarsson (1998), Vallin and Nissling (2000)
Melanogrammus aeglefinus	Egg size	Length	Hislop (1988), Trippel and Neil (2004)
Merluccius hubbsi	Egg size	Length	Macchi *et al.* (2006)
Merluccius merluccius	Egg size	Length	Mehault *et al.* (2010)
Morone saxatilis	Egg size	Weight	Zastrow *et al.* (1989)
Oncorhynchus keta	Egg size	–	Beacham and Murray (1985)
Perca flavescens	Egg size, larval quality	Length	Heyer *et al.* (2001), Lauer *et al.* (2005)
Perca fluviatilis	Egg size, larval quality	Length	Olin *et al.* (2012)
Pleuronectes americanus	Egg size	–	Buckley *et al.* (1991)
Pleuronectes platessa	Egg size	Weight	Kennedy *et al.* (2007)
Pomoxis annularis	Egg quality	Length	Bunnell *et al.* (2005)
Pseudopleuronectes yokohamae	Egg size	Length	Higashitani *et al.* (2007)
Salmo salar	Egg size	Length	Burton *et al.* (2013)
Salmo trutta	Egg size	Length	Ojanguren *et al.* (1996)
Sander vitreus	Egg size, egg quality	Length, age	Johnston and Leggett (2002), Wiegand *et al.* (2004), Johnston *et al.* (2007), Venturelli *et al.* (2010), Wang *et al.* (2012)
Scophthalmus maximus	Egg size	Weight	McEvoy and McEvoy (1991)
Sebastes carnatus	Larval quality	Age	Sogard *et al.* (2008)
Sebastes flavidus	Larval quality	Weight	Sogard *et al.* (2008)
Sebastes maliger	Larval quality	Weight	Rodgveller *et al.* (2012)
Sebastes melanops	Larval quality	Age	Berkeley *et al.* (2004b)
Sebastes mystinus	Larval quality	Length	Sogard *et al.* (2008)
Seriphus politus	Egg size	Weight	DeMartini (1991)
Stegastes partitus	Larval size, swimming performance	Length	Johnson *et al.* (2011)
Xiphophorus birchmanni	Larval size	Age	Kindsvater *et al.* (2012)

For studies where more than one maternal trait had a significant relationship with offspring traits, the maternal trait with the highest r^2 is reported. Listing more than one maternal trait indicates different results among studies for that species. The review by Heath and Blouw (1998) provides additional examples.

There is a wealth of literature examining variation in egg size in oviparous teleosts, and differences in egg size among stocks can be extensive (Chambers and Leggett, 1996). For example, Johnston and Leggett (2002) noted widespread variation in egg size among walleye (*Stizostedion vitreum*) in different lakes, potentially a consequence of variation in productivity and the environment into which larvae hatch. Although the degree of variation in egg size among females within a local population is typically less than that among populations, significant maternal effects have been observed in a diverse range of species, generally indicating an increase in egg size with maternal age or size (Table 2). Kamler (2005) suggested that egg quality and size follow a parabolic trend with female age or size, increasing as fish reach intermediate ages/sizes then decreasing as females reach maximum ages/sizes. Such a pattern may reflect elevated maintenance metabolism costs of older fish, which limits energy for egg production (Kamler, 2005). The absence of such a decline for the species listed in Table 2 may reflect an absence of very old fish in the range of samples examined in these studies.

Direct measurement of egg quality, usually in terms of lipid constituents, has been conducted less frequently, and egg size is often assumed to be a sufficient proxy for egg quality. Although there are notable exceptions, this assumption has support from a substantial number of experimental studies documenting a correlation of egg size with a variety of traits indicative of fitness during the egg stage, such as embryo growth rate, survival to hatch, and size at hatch (Blaxter and Hempel, 1963; Knutsen and Tilseth, 1985; Hinckley, 1990; Bernardo, 1996; Chambers, 1997; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Einum and Fleming, 2000). Larger egg size and better condition of yolk-sac and feeding larval stages in turn generally confer advantages of better swimming capabilities, faster growth, better sensory detection of both predators and prey, and overall higher survival (Miller *et al.*, 1988; Searcy and Sponaugle, 2001; Vigliola and Meekan, 2002; Fisher *et al.*, 2007).

For the few studies that have measured offspring constituents, those detecting maternal effects have generally found that eggs or larvae from older or larger mothers contain more energy reserves. In an extensive review of primarily freshwater species, Kamler (2005) concluded that egg quality in terms of proximate composition often increases with female age but not female size. In many species, offspring with greater lipid content or other indices of energetic quality were not derived from larger eggs or larvae. In the primitively live-bearing rockfish species (Family Scorpaenidae), size of larvae at parturition appears to be a conservative trait with minimal intraspecific variation, although several species have demonstrated a maternal effect of increased lipid stores in larvae produced by older or larger mothers (Berkeley *et al.*, 2004b; Sogard *et al.*, 2008). The amount of triacylglycerol lipids in the oil globule at parturition determines a larva's ability to resist starvation (Fisher *et al.*, 2007) and is also correlated with growth rates in the rockfish *S. melanops* (Berkeley *et al.*, 2004b). Gagliano and

McCormick (2007) found that egg size was conserved but lipid stores varied in the damselfish *Pomacentrus amboinensis* when food availability varied. Kerrigan (1997) found that smaller mothers of the same damselfish produce longer larvae but with lower yolk reserves than offspring from larger mothers (see also Maddams and McCormick, 2012). In lab experiments, Uusi-Heikkila *et al.* (2010) found that smaller female zebrafish (*Danio rerio*) produced larger eggs compared with larger females, but those eggs had higher mortality rates, again suggesting that size alone was not an accurate indicator of egg quality. Nonetheless, Cardinale and Arrhenius (2000) and Carr and Kaufman (2009) concluded that BOFFFFs and their eggs were the greatest contributor to recruitment success in Atlantic cod (but see Ottersen, 2008).

The underlying reason for the commonly observed increase in egg size or quality with maternal age or size is somewhat controversial. Is this pattern, an adaptation to the environment into which eggs will hatch, as suggested by Marshall *et al.* (2010), or a consequence of greater energy resources in larger females and a potential shift in the fecundity vs. egg size/quality trade-off as fish age (Roff, 1992)? Classic life-history theory suggests that this trade-off should be resolved around an optimal offspring size/quality for the expected environmental conditions encountered by early life stages (Smith and Fretwell, 1974). For a given offspring environment, mothers with more resources may maximize their fitness by simply producing more offspring. However, offspring environments may differ and environmental quality is thought to be inversely related to the degree to which investment in offspring results in greater offspring survival. Harsher environments should therefore select for larger offspring. There is extensive evidence suggesting that population level differences in egg size match the expectation of larger or higher quality eggs in lower quality larval environments (Johnston and Leggett, 2002; Castro *et al.*, 2009; Wang *et al.*, 2012).

Marshall *et al.* (2010) argue that one reason for observed maternal effects on offspring size may be a link between maternal phenotype and offspring environment. For example, in rockfish (genus *Sebastes*) younger mothers tend to produce lower quality larvae but release them later in the season (Sogard *et al.*, 2008), which may distribute their offspring into a more favourable environment than larvae produced earlier in the season by older mothers. Under this scenario, larvae would have equivalent fitness despite differences in energetic reserves provided by their mothers, and the expected survival of offspring would not differ with female size/age. This argument presumes that the number vs. quality trade-off does not differ with maternal resources. If, however, the shape of this trade-off varies with maternal resources, then younger or smaller females with low energetic reserves may shift allocation patterns and produce offspring of slightly lower quality while maintaining fecundity as high as possible. Evidence that this trade-off varies with female reproductive resources has been observed in three-spined stickleback (*Gasterosteus aculeatus*), where females with reduced energy reserves due to parasites had the same clutch biomass as unparasitized females, but shifted their allocation to produce larger numbers of smaller eggs (Heins, 2012). In this system, the larval stages would presumably encounter the same environmental conditions whether from parasitized or unparasitized mothers. Burton *et al.* (2013) similarly found that the fecundity/offspring size trade-off varied with maternal attributes in Atlantic salmon (*Salmo salar*).

The question of adaptive response vs. physiological constraints also pertains to changes in egg size for individual females within a spawning season. Batch spawners often produce progressively smaller eggs as the spawning season continues (e.g. Hislop, 1975; Ware, 1977; Kjesbu *et al.*, 1991; Macchi *et al.*, 2006). This pattern may be due to seasonal changes in production cycles (Cushing, 1967), suggesting an adaptive strategy that balances egg fitness with fecundity over the spawning season (Ware, 1977), or depleted energy reserves, indicating that bioenergetic demands result in reduced egg fitness in successive batches. The anchoveta (*Engraulis ringens*) off the coast of Chile exhibits the latter pattern, with egg size and lipid content declining over the spawning season, resulting in a decreasing trend in hatching success (Castro *et al.*, 2009). The decline in egg size over a spawning season has been found primarily in winter/spring spawners. Fall spawning European pilchard (*Sardina pilchardus*), in contrast, showed increasing egg size as the spawning season progressed (Daoulas and Economou, 1986). These authors did not proscribe an adaptive explanation for this difference, but more proximally, suggested that decreasing temperatures caused this response in egg development.

Parker and Begon (1986) developed theory to explain increased egg size with increased maternal size, based on density-dependent sibling competition that might arise with increased fecundity. Such a mechanism may be a factor for teleosts that spawn demersal eggs in cohesive nests, but seems unlikely for the many pelagic spawners that exhibit maternal size effects. Indeed, the model of Kindsvater *et al.* (2011), relevant to highly fecund fish that are likely to experience survival costs associated with reproduction, suggests scenarios that depart from the Smith and Fretwell (1974) model summarized above. In this case, younger females are predicted to reduce offspring size, thereby maximizing survival until the next opportunity to reproduce.

In summary, although there is substantial evidence that, all else being equal, offspring of BOFFFFs typically perform better than those of smaller females, additional studies are needed to determine whether the larger or better provisioned offspring produced by BOFFFFs have a higher probability of survival than offspring of younger and/or smaller females spawned at different times or places. New genetic approaches for matching parents and offspring hold much promise for such studies (e.g. Christie, 2010). For example, Beldade *et al.* (2012) found that larger female orange-fin anemonefish (*Amphiprion chrysopterus*) were more likely than smaller females to produce successful recruits and that fecundity alone was insufficient to account for the success of BOFFFFs, suggesting maternal effects on larval quality. In any case, we do not assert that maternal effects on offspring size or quality are universal in teleost fish. Rather, we believe that, because maternal effects have evolved in a diverse taxonomic range of species, removing older, larger fish from a population may have deleterious consequences for fisheries productivity. In years or locations with high-quality, food-rich larval habitats, larval fitness may be equivalent among individuals with varying levels of maternal provisioning. Likewise, in some environments, larger offspring or those with more energy reserves may potentially have lower fitness than smaller, less well provisioned eggs. Over the long term, however, we believe that continual contribution of higher quality offspring from older females provides one of the mechanisms that buffer survival of a larval cohort.

Benefits of maternal effects and old-growth age structure to fisheries productivity

Temporal variability in the conditions experienced by larvae is a basic characteristic of many aquatic ecosystems and a presumed

Table 3. Representative teleost species with the timing of annual spawning or parturition documented to be earlier and/or longer with increasing female age and/or size.

Species	Reference
Clupea harengus	Lambert (1987)
Engraulis encrasicolus	Millan (1999)
Gadus morhua	Hutchings and Myers (1993)
Hemiramphus balao	Berkeley and Houde (1978)
Hemiramphus brasiliensis	Berkeley and Houde (1978)
Melanogrammus aeglefinus	Wright and Gibb (2005)
Morone saxatilis	Cowan *et al.* (1993)
Pleuronectes platessa	Rijnsdorp (1994)
Sebastes crameri	Nichol and Pikitch (1994)
Sebastes entomelas	Stafford (2012)
Sebastes flavidus	Sogard *et al.* (2008)
Sebastes atrovirens	Sogard *et al.* (2008)
Sebastes melanops	Bobko and Berkeley (2004) and Sogard *et al.* (2008)
Sebastes mystinus	Sogard *et al.* (2008)
Trisopterus luscus	Alonso-Fernandez and Saborido-Rey (2011)

Reviews by Miranda and Muncy (1987), Trippel *et al.* (1997), and Wright and Trippel (2009) provide additional examples.

driver of the evolution of the long lifespans that produce old-growth age structure (Murphy, 1968; Longhurst, 2002). BOFFFFs often have earlier and/or longer spawning seasons than smaller, younger female fish, as documented in a variety of species (Table 3). Additionally, in multiple-batch spawners, older fish may produce more batches of eggs over a longer period each season, as documented in drum (DeMartini and Fountain, 1981), anchovy (Parrish *et al.*, 1986), striped bass (Secor, 2000a), haddock (Wright and Gibb, 2005), and sardine (Claramunt *et al.*, 2007), among others. For example, individual Atlantic cod can spawn over a range of 2–7 weeks, and by individuals spawning at different times, a population may spawn over a range of 4–15 weeks (Marteinsdóttir and Björnsson, 1999).

This temporal spread of reproductive effort provides a bet-hedging life-history strategy helping to ensure that some larvae are spawned at times of favourable environmental conditions, including high food availability (Cushing, 1990, as foreshadowed by Hjort, 1914) and/or low predation intensity (Bailey and Houde, 1989). Additionally, BOFFFFs may spawn in different locations than younger, smaller fish (reviews by Wright and Trippel, 2009; Hsieh *et al.*, 2010), providing spatial as well as temporal bet-hedging. Empirical evidence for bet-hedging includes settlement of plaice (*Pleuronectes platessa*) occurring over several weeks despite spawning occurring over several months (Hovenkamp, 1991). Likewise, the extensive occurrence of "sweepstakes reproductive success" (Hedgecock and Pudovkin, 2011) demonstrates the rarity of each individual contributing to recruitment in any given year. Evidence for the importance of BOFFFFs in bet-hedging includes the fact that first-time, late-spawning female haddock (*Melanogrammus aeglefinus*) contribute little to recruitment (Wright and Gibb, 2005; see also the state-based model of Wright and Trippel, 2009). The fact that young, late-spawning female black rockfish (*Sebastes melanops*) contribute substantially to recruitment some years yet not others is indicative of the hit-or-miss nature of recruitment in age-truncated stocks (Bobko, 2002, cited in Bobko and Berkeley, 2004). More directly, positive relationships are evident between the age diversity of spawners and subsequent recruitment success (Lambert, 1990; Marteinsdóttir and Thorarinsson, 1998; O'Brien *et al.*, 2003). Other empirical examples are provided in Secor's (2007) review. Thus, there is increasing evidence that old-growth age structure is a better index of the reproductive potential of a stock than simply SSB alone (Marshall *et al.*, 2003; Lambert, 2008). Overall, age truncation due to fishing may alter the timing and duration of annual reproduction by delaying and shortening the spawning season (Scott *et al.*, 2006), contributing to the observed increase in recruitment variability for stocks comprised of only younger spawners (Marteinsdottir and Thorarinsson, 1998; Secor, 2000b; Wieland *et al.*, 2000; Hsieh *et al.*, 2006).

Effects of maternal age/size on both offspring size/quality and relative fecundity may reflect higher body condition as females age. Many of the studies reporting significant effects in Tables 1 and 2 did not measure body condition, but we suspect that often energy reserves increase with female age and size, as first noted by Hjort (1914). Thus, BOFFFFs have more resources to apply to reproduction compared to younger/smaller females. The importance of energy accumulation by mature females was aptly demonstrated in Atlantic salmon by Reid and Chaput (2012), who found that females spawning in consecutive years had smaller eggs than females that skipped spawning for a year, presumably allowing the latter to acquire more resources for the years in which they did eventually spawn. In any case, recent explorations suggest that incorporating maternal effects into fisheries models are likely to be more useful than continuing to assume that all SSB is equivalent (e.g. Scott *et al.*, 1999; Berkeley, 2006; Lucero, 2008, 2009; O'Farrell and Botsford, 2006; Shelton *et al.*, 2012). In a modelling exercise, O'Farrell and Botsford (2006) found that, for typical long-lived fish, maternal effects result in large errors in estimates of lifetime reproductive success when there is a large difference in the mortality rate of larvae produced by young vs. old females. However, examining empirical data for black rockfish (*S. melanops*) from Berkeley *et al.* (2004b), they concluded that such errors in traditional management would be small for this species (O'Farrell and Botsford, 2006).

Age truncation and artificial selection caused by fishing

Because old-growth age structure can provide the benefits of maternal effects and other bet-hedging strategies reviewed above, it follows that BOFFFFs are a valuable component of stock productivity. However, fishing tends to differentially remove BOFFFFs because fishing both elevates mortality and changes the age/size-selective pattern of mortality within fished populations. Commercial fisheries tend to target phenotypes that are the most valuable or marketable (e.g. large fish). This focus, in turn, influences how and where fish are caught, which can lead to selective removal of certain phenotypes. An obvious example of how fishing may be selective is through net mesh size: a given mesh size will catch larger fish while allowing many smaller fish to escape. Gear types can also be selective in other ways. In addition to selecting on body size, passive gear types such as driftnets or longlines also tend to remove bolder individuals from the population (Biro *et al.*, 2004; Biro and Post, 2008). Even bait type and hook size will generate some degree of selection because the fish that are caught by these methods are fish that are both drawn to the bait and large enough to bite the baited hook (e.g. Millar, 1992; Myers and Hoenig, 1997). Other mechanisms of fishery selection may be less intuitive, but also very important (Millar and Fryer, 1999).

For example, larvae of many demersal species settle in shallow coastal regions, then slowly move offshore as they age and grow (e.g. North Pacific rockfish, Love *et al*., 1991). Given such ontogenetic habitat shifts, concentrating fishing effort by depth or location can cause artificial selection on age and size.

In addition to the direct effects of fishing practices causing selective mortality, fishing of course elevates mortality rates overall, often to high levels. Even if fishing mortality is constant with respect to age and body size, increasing the overall mortality rate can still result in selection favouring smaller size and earlier age at maturation (Stearns and Koella, 1986).

Although fishing can be strongly size selective, it is more informative to consider the selective effects that fishing can have on a suite of related life-history traits (e.g. growth rate, maximum size, lifespan, boldness, etc.). In this regard, it is useful to view fishery selection through the lens of life-history theory, which provides a framework for combining the selectivity of fishing practices with the effects of overall increases in mortality rates. Importantly, life-history theory allows one to evaluate how fishery selection interacts with natural patterns of selection. Life-history characteristics such as growth form and size/age at maturation evolve towards maximizing individual fitness, given the abiotic and biotic constraints a population experiences (Roff, 1992; Stearns, 1992). For example, patterns of natural (unfished) selection on body size at maturation are often stabilizing, such that size-related reproductive advantages (including maternal effects on offspring quality) are balanced by size-related delays in maturation that result in lower average survival to adulthood (Roff *et al*., 2006; Johnson and Hixon, 2011). In other words, there may be a trade-off between being large at maturation (which allows the production of more and better provisioned offspring) and the time it takes to attain a large size (greater development time results in a greater risk of dying before reproducing at all). By both increasing total mortality and changing patterns of size-dependent mortality, fishing can upset such balances and shift patterns of selection such that smaller fish are favoured (Allendorf and Hard, 2009). In essence, fishing mortality can alter the selective regime that a population experiences.

Whenever a population is fished, there is the potential for substantial changes in the phenotypic composition of the population. In the short term, fishing mortality tends to remove larger and older individuals (BOFFFFs) from the population. This removal often leads to strong truncation of age and size distributions within fished populations (Trippel, 1995; Levin *et al*., 2006; Sharpe and Hendry, 2009; Fisher *et al*., 2010; Stewart, 2011). Over longer periods (i.e. across generations), the distribution of phenotypes may change due to phenotypic plasticity and/or evolution. It is quite clear that over generations, life-history characteristics can change substantially within fished populations (e.g. Ricker, 1981; Jorgensen, 1990; Rijnsdorp, 1993; Trippel *et al*., 1997; Olsen *et al*., 2004; Rijnsdorp *et al*., 2005; Swain *et al*., 2007). However, it is often difficult to discern how much of the observed phenotypic changes are due to an underlying genetic response vs. a sustained, plastic response of phenotypes (Kuparinen and Merila, 2007). Long-term studies of wild populations tend to be observational. However, there is solid evidence from laboratory experiments that changes in mortality patterns can lead to evolved responses (Conover and Munch, 2002; Reznick and Ghalambor, 2005; van Wijk *et al*., 2013), and recent field studies have demonstrated changes in gene frequencies for a wild, fished population (Arnason *et al*., 2009; Jakobsdottir *et al*., 2011). In light of this evidence, it seems likely that at least some of the observed phenotypic changes in fished populations are due to an evolved response. Based on these conclusions, one would expect that fisheries-induced changes in phenotypes may not be easily reversible (Law, 2000, 2007; Conover *et al*., 2009; Heino *et al*., 2013).

When populations evolve in response to fishing and maternal effects are present, there may be long-term consequences for both the characteristics and the demography of offspring. Maternal effects may result in complex evolutionary responses of offspring characteristics, including time-lags, and responses that carry on after selection ceases (Kirkpatrick and Lande, 1989). Characteristics of offspring may also affect demographic rates. For example, sizes of larval and juvenile fish often strongly affect their survival rates (reviewed by Sogard, 1997; Perez and Munch, 2010). Fishery selection that changes the characteristics of adults may, through maternal effects, also change the characteristics of offspring. In turn, changes in offspring characteristics may strongly affect offspring survival and population replenishment. For example, Johnson *et al*. (2011) calculated that, over a single generation, a reasonable amount of fishery selection on adult size could lower larval size at hatching and reduce larval survival (over 90 d) by a factor of 0.86 (95% CI: 0.77–0.96). Although the rate of change in offspring characteristics is expected to slow over multiple generations (Kirkpatrick and Lande, 1989), these results suggest that, through correlated responses of larvae, fishery selection can result in a persistent reduction of larval survival. Maternal effects should therefore be considered when evaluating the long-term consequences that fishery selection will have for the dynamics of populations.

Deleterious consequences of age truncation for fisheries stability

Boom-and-bust cycles in exploited populations can lead to economic collapse and local extinction (Lande *et al*., 2003). Importantly, such erratic population fluctuations may be indicative of deleterious fishing effects well before obvious signs of stock collapse occur (Hsieh *et al*., 2006). It is increasingly well-documented that age-truncated fish stocks are more variable through time, and thus more susceptible to collapse, than populations with more intact age structure. This pattern is especially but not exclusively true for “periodic species” (*sensu* Winemiller and Rose, 1992) that exhibit relatively low early survival, late maturation, and high individual fecundity (such as cods and rockfish). In short, old-growth age structure fosters population stability, whereas age truncation often destabilizes population dynamics (Rouyer *et al*., 2012).

In the most comprehensive reviews to date, Hsieh *et al*. (2006, 2008) and Anderson *et al*. (2008) analysed the 50-year California Cooperative Oceanic Fisheries Investigations (CalCOFI) time-series (13 exploited and 16 unexploited species) and found that fishing significantly increased fluctuations of stocks in the southern California Current ecosystem. Anderson *et al*. (2008) tested three likely and non-mutually exclusive mechanisms proposed to explain this pattern. First, variable fishing intensity may directly cause population variability independent of any age-truncation effects (Jonzen *et al*., 2002). This hypothesis was falsified. Second, unlike BOFFFFs, small, young fish in age-truncated populations may not buffer environmental variability by “bet-hedging” reproductive output via a protracted spawning season (Murphy, 1968; Leaman and Beamish, 1984; Longhurst, 2002; Berkeley *et al*., 2004a; Hutchings and Reynolds, 2004; Hsieh *et al*., 2005, 2006). Third, the demographic characteristics of age-truncated populations (in particular, the per capita population growth rate) may be prone to unstable dynamics (Dixon *et al*., 1999;

Hsieh *et al.*, 2005). Although both the second and third hypotheses are due to age truncation, they generate subtly different predictions: the loss-of-bet-hedging hypothesis predicts that a population will more linearly track environmental variation, whereas the demographic-alteration hypothesis predicts clearly non-linear responses. For the CalCOFI data, the demographic-alteration hypothesis provided the better fit, although there was also evidence for the loss-of-bet-hedging hypothesis (Anderson *et al.*, 2008).

Modelling the dynamics of cod and herring populations, Rouyer *et al.* (2011) found that age truncation simultaneously increases the sensitivity of stocks to environmental fluctuations and lessens their response to variation in fishing intensity, resulting in "the paradox that heavily exploited, age-truncated populations are those most in need of careful management, but also are those least responsive to the effects of such management" (p. 3056). Murawski *et al.* (2001) reported similar results in modelling the collapse of Atlantic cod. In general, regardless of the specific causative mechanisms involved, age-truncated populations more closely track environmental fluctuations (Lambert, 1987; Marteinsdóttir and Steinarsson, 1998; Hutchings and Myers, 1993; Ottersen *et al.*, 2006; Hidalgo *et al.*, 2011, 2012), with associated destabilizing consequences for the fishery (Wright and Trippel, 2009). Additionally, a model and meta-analysis by Venturelli *et al.* (2009) of 25 exploited temperate and Arctic fish species subjected to age truncation indicated that old-growth age structure enhances population growth and thus supports higher exploitation rates. They concluded that severe age truncation is analogous to "forcing an iteroparous species to spawn as if it was semelparous [and] is unsustainable" (p. 923).

Age truncation also inhibits stock resilience over time-scales longer than annual production. The extremely high fecundity of teleost fish, the commonality of relatively long lifespans, and the high variability of recruitment in annual cohorts all suggest that individual reproductive success is rare and episodic. Recent technological advances in genetics have allowed quantification of effective population size (N_e) and estimations of the proportion of adults that successfully contribute to subsequent generations. Hauser and Carvalho (2008) report surprisingly low N_e in a taxonomically diverse range of marine species, suggesting that a large proportion of mature adults are unsuccessful at producing surviving progeny. Based on the evidence of maternal effects outlined above, they suggest that only older spawners ready in years of excellent recruitment may have a chance to become rare "sweepstake winners". For a 28-year time-series of pelagic juvenile rockfish surveys, Ralston *et al.* (2013) found a striking pattern of increased individual size, coherent among the ten most common *Sebastes* species, in years of high abundance. This result suggests that, in environmentally favourable years, larvae released earlier in the reproductive season had particularly high survival. Because older, larger rockfish females tend to release larvae earlier than younger, smaller females (Nichol and Pikitch, 1994; Bobko and Berkeley, 2004; Sogard *et al.*, 2008), it is likely that much of the production in high-recruitment years came from BOFFFFs. In contrast, when environmental conditions were not favourable for early spawners, much of the production was likely derived from younger females, with reduced offspring abundance despite the presumably greater amount of SSB compared with older females.

Repeated spawning over many years increases the likelihood that an individual's offspring will encounter a favourable environment in at least one of those years. For species with highly sporadic recruitment success, the long-term survival of older females provides a "storage effect" of reproductive potential whereby elder and overlapping age classes of the population can out-live extended periods of poor recruitment, ready to take advantage of favourable conditions when they return, thereby fostering population persistence (Warner and Chesson, 1985). This phenomenon was implicit in Hjort's (1914) recognition that unusually strong year classes of herring sustained recruitment over subsequent years. Indeed, there is a well-documented positive relationship in a broad variety of exploited fish (excluding flatfish) between recruitment uncertainty and longevity (reviews by Secor, 2007, and Longhurst, 2002, 2010). However, it is only recently that managing for storage effects in fished populations by maintaining old-growth age structure has been seen as important for fisheries stability (Frank and Brickman, 2001; Berkeley *et al.*, 2004a; Field and Francis, 2006; Secor, 2007; Longhurst, 2010). The storage effect is likely to be particularly important at the margins of species geographical ranges, where successful recruitment is often rare (MacCall, 1990).

Approaches and challenges of managing for old-growth age structure

The empirical evidence summarized here indicates that, for a broad diversity of exploited marine fish, populations characterized by old-growth age structure with a substantial abundance of BOFFFFs are more stable, more predictable, and less prone to overfishing collapse than age-truncated stocks (Figure 3). Given that at least 30% of the world's fisheries stocks are overexploited (FAO, 2012), the onus is on fisheries scientists and managers to better conserve BOFFFFs than we have in the past. How can this goal be accomplished and why have we not yet done so already?

The pattern of selective fishing has profound effects on the age structure, productivity, and stability of an exploited stock (Brunel and Piet, 2013). Berkeley *et al.* (2004a) reviewed three management approaches that can help to conserve BOFFFFs in an exploited population: (i) very low rates of fishing mortality, (ii) slot size limits in which there is both a minimum and maximum size for retention, and (iii) marine reserves, where old-growth age structure can develop, spawn, and seed nearby fished areas unhindered. In the first approach, reduced exploitation will allow more fish to reach old age. However, to be effective this strategy may require fishing mortality to be reduced to prohibitively low and economically unfeasible levels. This approach successfully rebuilt populations and restored old-growth age structure in Atlantic striped bass (*Morone saxatilis*), yet involved severe fishing restrictions, including a virtual moratorium lasting 5 years (Richards and Rago, 1999; Secor, 2000b).

The second option—a slot size limit—is feasible only for species that can be released unharmed after capture, typically recreational fish (e.g. Arlinghaus *et al.*, 2010). Many deepwater fish typically do not survive post-capture release due to the internal trauma of expansion and rupture of the swimbladder during capture. Swimbladder or not, the condition of many fish after capture, especially in commercial fisheries, is typically too poor to ensure subsequent survival.

The final option to conserve BOFFFFs and prevent age truncation—marine reserves—has the greatest potential to allow at least a segment of a population of a demersal species to age naturally and export larvae produced by a broad age and size range of spawners (Murray *et al.*, 1999; Berkeley *et al.*, 2004a; Berkeley, 2006; Edwards and Plaganyi, 2011). Importantly, the "seeding effect" of marine reserves in a fisheries context—larvae being

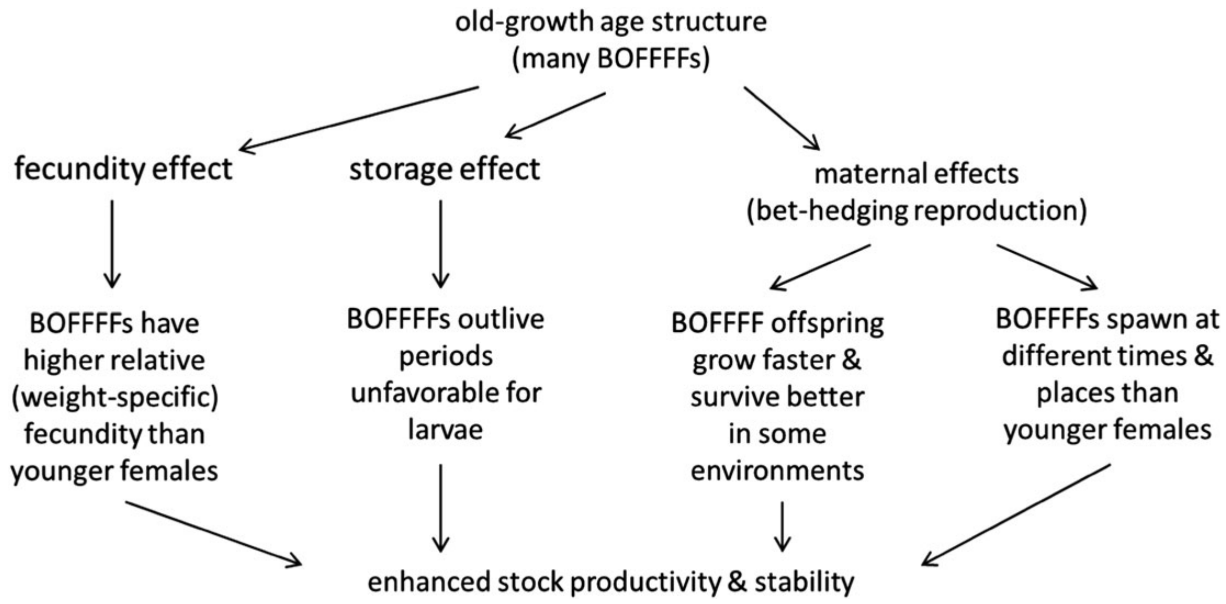

Figure 3. Summary of the benefits to stock productivity and stability provided by old-growth age structure, which includes many BOFFFFs. These benefits are negated by severe size and age truncation (removal of BOFFFFs) caused by fishing, which can further result in fisheries-induced evolution that is difficult to reverse once a stock has collapsed.

spawned inside reserves, dispersing and replenishing fished populations outside—has now been demonstrated using novel genetic methods (Christie *et al.*, 2010; Harrison *et al.*, 2012; Almany *et al.*, 2013), so the value of BOFFFFs in the context of marine reserves is now clear. However, the marine reserve approach is viable only for species whose post-settlement home ranges remain largely within the boundaries of the reserve, which fortunately includes a broad variety of demersal species (reviews by Halpern and Warner, 2002; Halpern, 2003; Gaylord *et al.*, 2005; Claudet *et al.*, 2008; Lester *et al.*, 2009). Given that recruitment may come from restricted temporal and spatial oceanographic windows that change from year to year (review by Berkeley *et al.*, 2004a), such management should include efforts to preserve minimal spawning stock sizes over the entire geographic range of the stock (e.g. Larson and Julian, 1999). Networks of marine reserves, where replicate sites include a variety of seabed habitats in each biogeographic region, therefore offer the greatest potential to conserve old-growth age structure in a multispecies assemblage of exploited demersal species.

Why—100 years after Hjort (1914) first inferred indirectly that parental effects may be important in replenishing fishery stocks—have there been no widespread efforts to conserve old-growth age structure and the increasingly obvious fishery benefits provided by BOFFFFs? Perhaps the answer lies in the real and perceived difficulties of implementing the above management approaches. Uniformly low exploitation levels are seldom if ever implemented until reactive, emergency stock-rebuilding measures are in place following stock collapse. Slot limits are typically difficult to implement, especially in commercial fisheries. Marine reserves worldwide are increasingly well documented to provide fisheries benefits from at least a biological perspective (Halpern and Warner, 2002; Halpern, 2003; Gaylord *et al.*, 2005; Claudet *et al.*, 2008; Lester *et al.*, 2009; Christie *et al.*, 2010; Harrison *et al.*, 2012), yet the collective psyche of the combined fishing/fisheries science/fisheries management community has historically been unwilling to consider proactive, permanent, spatial closures to ensure that fisheries benefit from the reproductive capacity of old-growth age structure. Fortunately, change is in the air. For example, recent stock assessments of 12 of 19 rockfish species (genus *Sebastes*) incorporate age or size-dependent relationships with relative fecundity, thus accounting for some documented BOFFFF effects (http://www.pcouncil.org/groundfish/stock-assessments/by-species/). Overall, following many authors cited here, we believe that it is time for a sea change in worldview regarding the value of old-growth age structure.

Acknowledgements

We dedicate this essay to the memory of Steven A. Berkeley, whose pioneering research on the maternal effects of BOFFFFs and their fisheries implications was seminal to the ideas presented herein. Authors are listed alphabetically because contributions were equal. This is Contribution Number 2013-20 from the Department of Biology at the University of Hawaiʻi at Mānoa.

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Handling editor: Howard Browman

ICES Journal of Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2186–2197. doi:10.1093/icesjms/fsu094

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Temporal variation in winter flounder recruitment at the southern margin of their range: is the decline due to increasing temperatures?

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Able, K. W., Grothues, T. M., Morson, J. M., and Coleman, K. E. Temporal variation in winter flounder recruitment at the southern margin of their range: is the decline due to increasing temperatures? – ICES Journal of Marine Science, 71: 2186–2197.

Received 27 August 2013; revised 29 April 2014; accepted 30 April 2014; advance access publication 10 June 2014.

The southern-most stock of winter flounder (*Pseudopleuronectes americanus*), a cold temperate species of the Northwest Atlantic, has not recovered from overfishing despite continued restrictive measures, and appears to be contracting northward. We regressed larval and settled juvenile abundance (after accounting for adult and larval contribution to variation, respectively) on temperature over several decades from collections in New Jersey, the United States, at the southern edge of their range to determine if increasing temperatures during the first year of life were responsible for this contraction. A significant stock–recruitment relationship at both stages was moderate, explaining 27.5% of the variance for larvae on adults and 20.6% for juveniles on larvae. There was no significant effect of average monthly temperature in explaining variance of the residuals for larvae, or of degree day on explaining the abundance of residuals for juveniles over a months-long settlement period. However, in both cases, residuals were widely distributed at cold temperatures, while they were always low at warm temperatures. Thus, years in which spring temperatures were warm (5–7°C for February, 7–9 for March, and 11–20 for May) always experienced poor recruitment. This threshold effect may result from an intersection with predators in response to temperature, and this may play a more important role than heat stress in determining recruitment success.

Keywords: climate change, larvae, recruitment, temperature, temporal variation, winter flounder.

Introduction

With prompting by Hjort (1914, 1926), there has been extensive literature addressing our inability to understand the factors influencing fish recruitment (Browman, this volume; Chambers and Trippel, 1997; Houde, 2008; Doyle and Mier, 2012). An emerging consensus is that there are many factors, especially in the early life history stages, that contribute to this variability. These include natural mortality of the larvae and juveniles due to starvation, predation, adverse transport, and habitat degradation, potentially including climate change, and others (see other papers in this volume). It is also possible that adults may be overfished to the point that reproduction is hampered by depensation, (Liermann and Hilborn, 2001; Marato and Moran, 2014). Many of these factors may be contributing to the decline in spawning-stock biomass (SSB) and landings (Figure 1a and b) of winter flounder (*Pseudopleuronectes americanus*), from the Southern New England–Mid-Atlantic (SNE/MA) stock. The species is commercially and recreationally important along the western North Atlantic margin. Overfishing was credibly blamed for the precipitous decline of this stock in the 1980s, but poor recruitment rather than overfishing in the late 1990s and 2000s contributed to its failure to recover (Northeast Fisheries Science Center, 2011). This species has been reported from Georgia (the United States) to Labrador (Canada) and is cold adapted with antifreeze proteins (Collette and Klein-MacPhee, 2002). National Marine Fisheries Service (NMFS) trawl surveys indicate that the southern limit of the range is between Cape Hatteras, North Carolina, and Cape Cod, Massachusetts (the United States; Able and Fahay, 2010) and the centre of abundance is north of New Jersey (Perlmutter, 1947; Scott and Scott, 1988). This is supported by evaluations in New

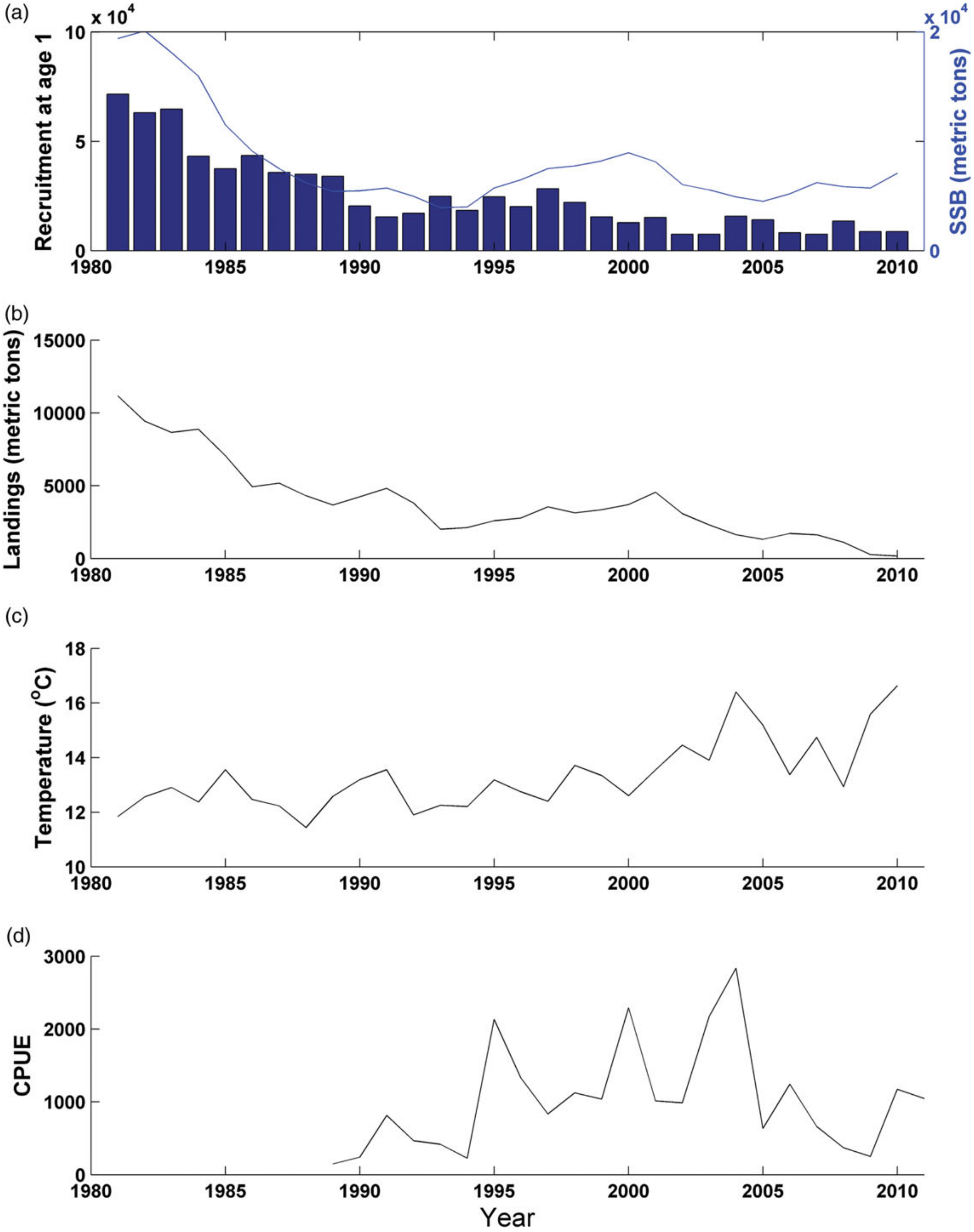

Figure 1. Annual variation in SSB (line) and recruitment (bars) (a), and landings (b) for the Southern New England – Mid-Atlantic Bight stock, temperature behind Little Egg Inlet (c), and catch per unit effort (CPUE) for larval abundance at Little Sheepshead Creek behind Little Egg Inlet (d). See Figure 2 for New Jersey locations.

Jersey, which have consistently indicated that the juveniles and adults are less abundant in the southern and more abundant in the northern part of the state (Scarlett, 1991; Scarlett and Allen, 1992; Sogard *et al.*, 2001).

A species-wide and local population shift in the distribution appears correlated with a decline in abundance for the SNE/MA stock (Collie *et al.*, 2008; ASMFC, 2013). The decline is evident in the change in SSB, a frequently used index of population status (Danila, 2000; Brodziak *et al.*, 2001), and landings from a long time-series from NMFS (Figure 1a and b). The centre of the adult distribution has shifted further north with warming temperatures (Nye *et al.*, 2009; Lucey and Nye, 2010; Pinsky and Fogarty, 2012). Larvae for populations in the SNE/MA stock are hatched from benthic eggs deposited in estuaries and juveniles continue to grow in these natal estuaries and be exposed to temperature fluctuations there (Jeffries and Johnson, 1974; Laurence, 1975; Rogers, 1976; Chant *et al.*, 2000; Keller and Klein-MacPhee, 2000; Sogard *et al.*, 2001; Curran and Able, 2002; Manderson *et al.*, 2007). Thus, recruitment success is expected to be constrained by local (watershed scale) phenomenon; yet, the annual abundance of juveniles in southern New England has become synchronized by very large-scale events (Manderson, 2008). This possibly homogenizes an otherwise diverse recruitment portfolio (Secor, 2007; Kerr *et al.*, 2010) and destabilizes population dynamics. Over the same period, estuarine temperatures have increased with fewer cold winters and increasing annual average water temperatures (Figure 1c, Able and Fahay, 2010) raising the suspicion that climatic factors may have played a role, at least in New Jersey, during 1989–1999 (Sogard *et al.*, 2001). Despite these changes, there was no evidence of a decline in larval abundance at a site within the Great Bay–Barnegat Bay estuaries over the period from the late 1980s to 2006 (Figure 1d, Able and Fahay, 2010). In fact, larval abundance has been among the highest, relative to the long-term average, for several years since 2000. Juvenile abundance has also been high during several of these years. Contradictory signals in reproductive success can arise from a number of mechanisms, including those that are very specific to particular life history stages (e.g. Lough and O'Brien, 2012), or assessment practices that conflate substocks or subpopulations that actually have their own semi-independent dynamics (Hillborn and Walters, 1992).

In the Great Bay–Barnegat Bay estuaries in southern New Jersey, larvae occur in well-defined peaks in April and May (Witting *et al.*, 1999; Able and Fahay, 2010), but they can also occur on the inner continental shelf during March and April (Able and Fahay, 2010). Occurrence in the coastal ocean is supposedly due to outwelling of larvae from estuaries (Smith *et al.*, 1975); but, findings based on gonadosomatic indices by Wuenschel *et al.* (2009) raise the possibility of spawning in the ocean, a divergent life history strategy with examples in northern stocks (Collette and Klein-MacPhee, 2002; DeCelles and Cadrin, 2010). Winter flounder are among the most abundant species as larvae in the Great Bay–Barnegat Bay estuaries, with rankings of 1–6 out of 80+ species during 1989–2006 (Able and Fahay, 2010). As juveniles and adults they make seasonal, temperature-dependent migrations between the estuary and the ocean, at least in the southern portions of their current range such as off New Jersey (Phelan, 1992; Able and Hagan, 1995; Wuenschel *et al.*, 2009), apparently to avoid warm summer temperatures, although some may stay and tolerate these conditions in New York estuaries (Olla *et al.*, 1969; Sagarese and Frisk, 2011).

In an attempt to resolve contradictory signals from stock surveys and larval abundance, we reevaluated the status of winter flounder in the Great Bay–Barnegat Bay estuaries based on larval and juvenile time-series of over 25 and 22 years, respectively, relative to estuarine water temperatures. This time-series analysis approach has previously provided some predictive capability for winter flounder in other southern New England and mid-Atlantic estuaries (Jeffries *et al.*, 1989; Collie *et al.*, 2008; Rothschild and Jiao, 2011). In this case, we explicitly recognize that the simple relational links between SSB do not relate directly to progeny over the same area as that of the recognized stock; segregation into populations with their own dynamics could result from targeted fishing or differential migration and habitat use. The spawning capacity of adults may be best represented by smaller units for which only local measures apply. This may be especially relevant between the survival of the larvae and spring temperature of their habitat during development, and thus their recruitment to the settled juvenile phase. The relationship between juvenile survival and temperature may also be important over the ensuing summer as fish become estuarine residents. In recognizing both the distance we have come and the distance we have yet to go since Hjort (1914) first posited predictability for stock–recruitment (S–R) relationships, this remains an exploratory effort but is structured on a logical progression of hypothesis testing.

The first question in this exploratory series is broadly stated as*: What is the proper sampling unit for adults when attempting to quantify S–R relationships?* The phenomenon of adult segregation into stocks during spawning was recognized by Hjort (1914, 1926) and is practiced by fisheries managers today, but the information is not always complete or practical to apply. Thus, the southern-most federal winter flounder management unit, the SNE/MA stock, may be overly broad as a unit for examining S–R relationships in New Jersey. Fortunately, a state survey contributes to our understanding of that stock and is spatially discrete (shallower) from the federal survey (deeper). The surveys are designated *a priori* on an independent geo-political (federal vs. state waters) basis that divides sampling into broad vs. regional zonal and bathymetric constraints. These happen to coincide also with bathymetric features that topographically steer major oceanographic features and differentially influence temperature over the survey areas, namely, the bathymetric foot of the cold pool (see study site description below) and the Hudson Submarine Canyon (Figure 2). Thus, we have an *a priori* regionally defined biomass survey subset off New Jersey to which we can link a New Jersey recruitment signal.

The next question is broadly stated as: *What is the relationship between estuarine temperature and larval abundance?* A mechanistic relationship is posited by the metabolic theory of ecology, in which increasing temperature increases metabolic rate first towards increased performance and then eventually towards one that is unsustainable or ecologically non-competitive, given a particular enzyme kinetic (under genetic control) and organism size (Allen *et al.*, 2002; Ernest *et al.*, 2003). The empirical quantification of this relationship for individual species such as winter flounder and its contribution to variation is desirable to prediction for fisheries management. Thus, we erect the specific null hypothesis H_01: Larval abundance, after accounting for adult contribution, is not related to winter temperature. Following the life history stages, the next question is then broadly stated: *What is the relationship between temperature and juvenile abundance in the estuary?* We erect the specific null hypothesis H_02: Juvenile abundance, after accounting for larval supply, is not related to spring temperature. This serial approach (as opposed to a multiple regression approach) recognizes that such relationships, if they exist, may be stage-specific and sequential.

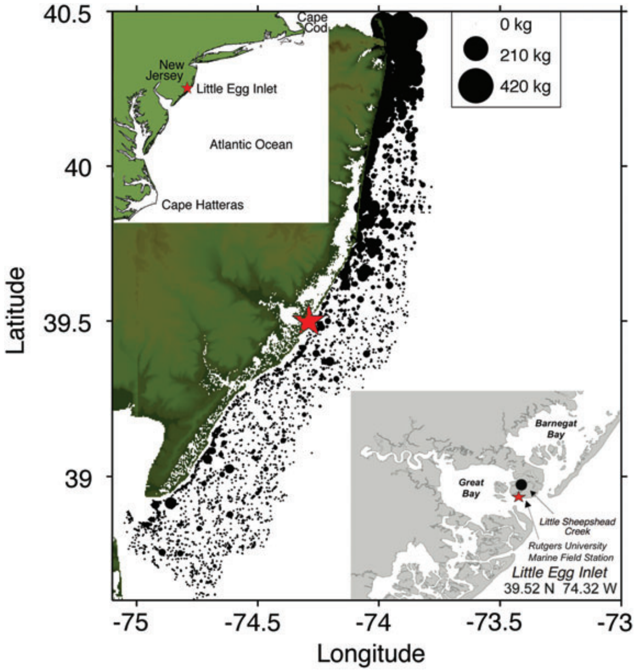

Figure 2. Cumulative distribution of relative abundance (kg tow^{-1}) of winter flounder along the coast of New Jersey in all seasons from 1989–2013 in New Jersey Department of Environmental Protection, Bureau of Marine Fisheries trawl survey. Upper inset indicates the position of the study site in the Middle Atlantic Bight. A star marks the location of the sampling site for larval and juvenile winter flounder (see lower inset for further details).

Material and methods

Study site

The range of winter flounder covered by the SNE/MA stock designation is the Middle Atlantic Bight (MAB) and extends from estuaries seaward to at least the continental shelf/slope break and from Cape Cod in the north to Cape Hatteras in the south (Figure 2). The circulation is distinct from that of the Gulf of Maine to the north and the Southeastern United States Continental Shelf to the south and has been called “estuarine” owing to strong buoyancy-driven effects from three very large estuaries (Hudson River, Delaware River, Chesapeake Bay), flow of cold water around Cape Cod that persists as far southward as the mid-shelf “cold pool”, and the introduction of warm saline Gulf Stream water from the southeast through various mechanisms (Beardsley *et al.*, 1976; Hare *et al.*, 2002). It has the highest annual temperature range of any oceanographic province and this is reflected by a seasonally diverse assemblage of subtropical to boreal fish species in the region’s estuaries (Able and Fahay, 2010). The apex of the shoreline bend defining the western edge is the New York Bight, from Long Island, New York, to New Jersey and split by the Hudson Submarine Canyon. In the southern part of the New York Bight is Barnegat Bay, a shallow (average depth <2 m, range 1–6 m) barrier island lagoonal system separated from a similarly shallow drowned river valley estuary, Great Bay, by a peninsular land mass, Sheepshead Meadows. The peninsula splits the two estuaries at their common important oceanic inlet, Little Egg Inlet (Figure 2). On flood tides, one source of exchange between these estuaries is the flow from southern Barnegat Bay, which is well mixed (Carpenter, 1963; Chizmadia *et al.*, 1984) into Great Bay through Little Sheepshead Creek and other thoroughfares (Charlesworth, 1968; Chant *et al.*, 2000). The tides are semi-diurnal with highest velocities at Little Egg Inlet (>2 m s^{-1}; Kennish, 2001). Water temperature ranges annually from −1.4 to nearly 30°C (Kennish, 2001).

Larval and juvenile sampling

Winter flounder larvae were collected with a 1 m diameter (1 mm mesh) circular plankton net at the bridge over Little Sheepshead Creek (3.8 km from Little Egg inlet; Figure 2). The site has been continuously in use with the same sampling protocol since 1989 (Able and Fahay, 1998; Witting *et al.*, 1999). The net was deployed with a General Oceanics flowmeter to a depth of ∼1.5 m. Collections were during the night-time flood tide for three consecutive 30 min sets (see Witting *et al.*, 1999, for more details). Fish abundance was standardized to effort as sample density (individuals 1000 m^{-3}) by calculating sample volume from the flow value and net diameter. Long-term trends in the timing and abundance of larval winter flounder were previously reported up to 2006 (Able and Fahay, 2010). The annual patterns of winter flounder larval abundance at the Little Sheepshead Creek long-term sampling site are likely to be indicative of larval supply because the larvae are annually available, abundant, and represented by all developmental stages. In addition, the timing of sampling for larvae in April and May is consistent with the patterns of occurrence elsewhere in the adjacent Barnegat Bay and Great Bay estuaries (KWA, unpublished data). Further, the late stages of development, which are likely to be indicators of year-class strength (Houde, 2008), are well represented and a source for settlement in the area (Witting, 1995; Chant *et al.*, 2000; Sogard *et al.*, 2001). This same sampling programme has proven useful for assessing the late larval abundance of other estuarine resident species as well (Able *et al.*, 2006, 2011; Able and Fahay, 2010) and as an index of climate change (Able and Fahay, 2010). Physical variables were recorded at deployment and retrieval of collectors. In most instances, a Yellow Springs Instrument (YSI) datalogger was used to record temperature (°C) and salinity (ppt), although in some cases, we used a thermometer. Long-term temperature averages were based on hand-held thermometer readings at Rutgers University Marine Field Station (RUMFS) (1989–1995) and YSI dataloggers in Great Bay (see below).

Sampling for settled juveniles occurred weekly from 1992 to 2013 in the boat basin of the RUMFS at the tip of the Sheepshead Meadows peninsula near Little Egg Inlet (Figure 2). Wire mesh traps (45 cm long, 23 cm diameter, 6.4 mm mesh, typically six, but up to 17) were deployed continuously and retrieved two to five times per week since 1992 (see Able *et al.*, 2005, for additional details). All individuals were counted and measured (TL mm) and then released at the point of capture. Abundance is standardized as monthly catch-per-trap (CPUE). Temperature and salinity were recorded at the time of capture.

Monthly temperature means for use in the analysis of juvenile recruitment patterns were calculated from two data streams to obtain the complete time-series. From 1989 until 1997, temperature was measured daily at midday at the mouth of the RUMFS boat basin. In 1996, a series of YSI dataloggers was established in the Great Bay estuary as infrastructure of the Jacques Cousteau National Estuarine Research Reserve’s (JC NERR) System-Wide Monitoring Program (SWMP), which is managed by standards and protocols common to the entire National Estuarine Research Reserve System

(Kennish 2004). One of those dataloggers (designated B126) is situated near the boat basin entrance and experiences the same water mass flows that service both the RUMFS boat basin and Little Sheepshead Creek. From 1998 to 2012, the annual monthly temperature mean was calculated from the datalogger, which was sampled at half-hour increments. Means calculated from the two data streams were compared for each month during which there was a complete dataset between 1996 and 1997. Deviations in any pair of observations averaged 0.1°C with a range of -0.49 to 0.76 and absolute values of the monthly mean differences were <0.26. Only SWMP data were used beginning in 1998.

Adult biomass index

The biomass of winter flounder on the continental shelf was measured in New Jersey state waters by the New Jersey Department of Environmental Protection (NJDEP), Bureau of Marine Fisheries as kilogramme of winter flounder by trawl station standardized to the trawl distance from 5 annual surveys (January, March, June, August, and November). This estimate is not the same as SSB because it includes immature females (<3 years old) as well as males. However, immature fish are smaller than mature fish and contribute proportionally less to the mean weight relative to their individual count and we assume that the sex ratio remains similar among year classes. All the seasonal surveys are important in measuring total biomass because fish are differentially vulnerable to the survey through the seasons. However, since winter flounder in New Jersey spawn beginning in February and into at least late March (Able and Fahay, 2010), we feel that the measure of fish that might participate in spawning in a particular winter is best assessed based on the winter (January and March) surveys for that year and the summer/autumn (June–November) surveys of the preceding year. For that reason, we recombined the quasi-bimonthly biomass estimates into nominal yearly estimates on that basis. We calculated the geometric mean CPUE on a per-survey basis, which de-emphasizes the weight of sporadic very high catches in individual trawls, and then calculated the nominal annual biomass as the arithmetic mean of those surveys.

Data analysis

We plotted both larval and juvenile abundance as time-series, so that patterns of increased or decreased agreement could be viewed against a temperature time-series. Next, we accounted for the effect of abundance of the previous life stage before testing the temperature effect. We accounted for the potentially important influence of adult biomass on larvae using ordinary least-squares regression of larval density on the NJDEP biomass index. Visual inspection of the biomass index against larval CPUE (emulating S–R) plots assisted by regression tree analysis found a best fit single node for a change in S–R phase. However, this node separated only the single highest biomass index data point from all others as a possible indication of biphasic modes (Duffy-Anderson *et al.*, 2005). Other than this single point, there was no evidence of curve flattening or depression at high biomass values (potential indicators of compensation or depensation or carrying capacity, Marato and Moran, 2014) that would have been better fit with a Beverton–Holt model. We tested the autocorrelation function (ACF) in the residuals for departure from noise allowing a maximum 5 year lag to allow for the bulk of a cohort of spawners to progress through the population. Likewise, we accounted for dependence of juvenile abundance on larval abundance from 1989 to 2012 by the same method. Although the larval-settled juvenile recruit relationship lasts approximately weeks instead of years, we again tested the ACF among years in consideration of the possibility that the nursery habitat itself had legacy conditioning effects on the inter-annual time-scale. The residuals of the juvenile-larval regression were then used to test temperature effects on larval density and juvenile CPUE, respectively.

Since the coastal ocean off New Jersey experiences extreme seasonal variability in water temperature (Beardsley *et al.*, 1976), we recognize that slight changes in the timing of spring warming could hide important differences in individual monthly temperatures, as could the mean of spring temperatures. Whereas the egg and larval duration is generally weeks to a month each (Sogard *et al.*, 2001), and larvae move generally with the water mass in which they are sampled, settled juveniles are resident for many months and experience tidal flows moving over them that can vary by as much as 8°C daily during some parts of the year. Therefore, before proceeding with regression on temperature, we plotted and examined by pairwise correlation the relationship of the individual consecutive mean monthly temperatures of the spawning, incubation, larval, and settlement period (approximately February and March, March and April, and April and May, respectively) over the 25-year time-series for which we had both data. These inspections help to determine whether the mean annual spring temperatures are reliable indicators of episodically driven temperature phenomenon and whether the rates of warming, rather than just the absolute temperatures, are changing. Based on those results (below), we examined the relationship of larval density on individual monthly mean temperatures, rather than yearly mean spring temperatures, by regression analysis.

Since the duration of the juvenile stage (months vs. weeks for larvae) confounds the use of mean monthly temperatures, we used a degree day estimate as the independent variable. Degree day (°D) is the cumulative daily difference between a biological reference temperature and all temperature measures of a day (minimum 2, but 48 per day in this case). Thus, it acts as an exposure index. Multiple daily temperature readings were only available for a subset of the data, being those dates after the SWMP array was functioning (beginning 1996 and when the logger was kept in the water throughout winter and spring with a minimum of large gaps). Selection on this basis yielded 9 years (1997–2002, 2006, 2008, 2012). To avoid biases arising from different daily or longer gaps during this annual period of rapidly rising mean daily temperature, we used data only from the intersect of the day-of-year from among these 9 years, starting March 1 through June 30. This yielded 82 day-of-year dates common to all 9 years. The biological reference temperature was set at 10°C. This value is debatable (see Laurence, 1975; Chambers *et al.*, 2001; Discussion) but it provides a scalar to produce the index for regression, and as such the regression is sensitive to the difference among observations and not the actual value. Statistical analyses were performed in MATLAB with scripts native to that software (corr.m, regress.m, RegressionTree.fit, autocorr.m, The Mathworks, Natick, MA, USA).

Results

Long-term variation in larvae and juveniles

Abundance of winter flounder larvae in the plankton at the Little Sheepshead Creek collection site ranged from 0 in summer through spring highs of up to 975 ind. 1000 m^{-3} (average of all three nets in one night's sampling) in May. The single greatest measured density was 1998 ind. 1000 m^{-3} in May 2004. Peak abundance

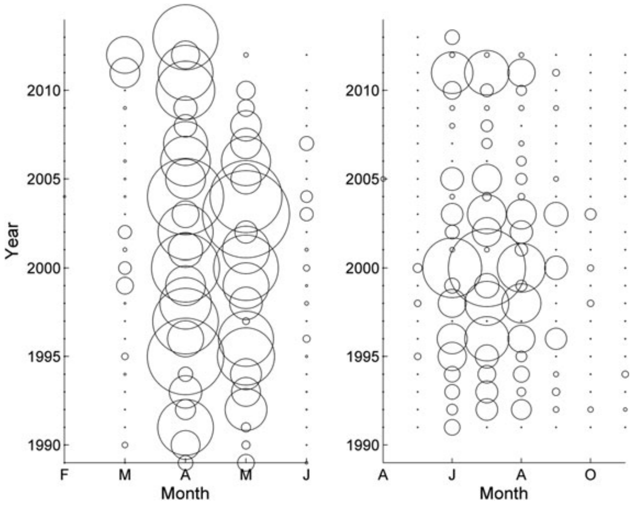

Figure 3. Bubble plot of the timing of arrival (capture) of larval (left) and juvenile (right) winter flounder by plankton net at Little Sheepshead Creek and trap at Rutgers University Marine Field Station boat basin, respectively, between 1998 and April 2013 for larvae and between 1991 and 2012 for juveniles. Bubble size is scaled to abundance. Solid dots show samples without any captures. No captures were made in months that are not shown, although sampling continued throughout all months of each year.

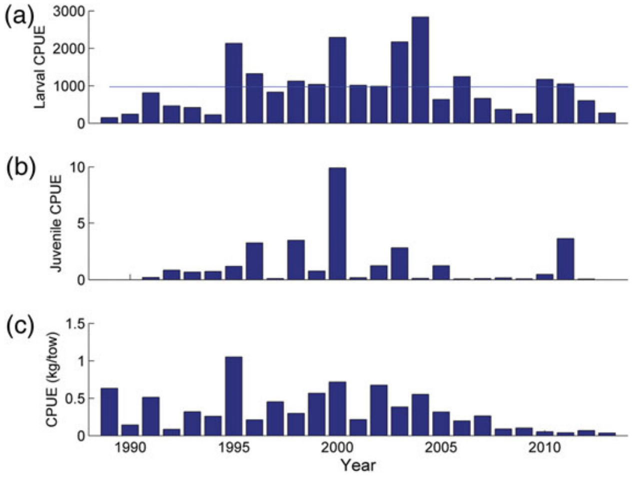

Figure 4. Annual density of larval winter flounder from plankton samples at Little Sheepshead Creek behind Little Egg Inlet (a), abundance (CPUE) of juvenile winter flounder from traps from the Rutgers University Marine Field Station boat basin (b), and estimated adult biomass based on CPUE of New Jersey Department of Environmental Protection, Bureau of Marine Fisheries trawl survey captures along the coast of New Jersey (c).

was always in either April or May, and for the most part, a high April abundance corresponded to a high May abundance in the same year and *vice versa* (Figure 3). Exceptions were in 2011 and 2012, when peak numbers were in April and an unusually high abundance occurred in March, but very few were captured in May. In 6 years, a few individuals were also collected in June, and these generally corresponded to years when they were also abundant in April and May.

There was pronounced annual variation in the abundance of winter flounder larvae (Figure 4). Peak annual abundance over the 24-year period was in 2004, ending a generally abundant period. From 1995 until 2004, density was lower-than-average in only a single year. The magnitude of these positive deviations from the mean was greater than that of the negative deviations, with the 11 total positive deviations balancing 13 negative deviations (one was at the average). In rank order overall, the pattern of larval abundance corresponded fairly well with that of the trawl survey biomass, which had a period of peak abundance from 1995 to 2003 for the time span matching that for larvae. Regression of the larval density on the trawl survey biomass accounted for moderate variation ($R^2 = 0.275$) and was highly significant ($F = 8.703$, $p = 0.007$). The ACF of residuals did not depart from random (range = -0.5165 to 0.3013, 95% bounds = ± 0.667) and so were not built into the ensuing regression model.

Juvenile winter flounder were available to traps generally by June, although a few occurred as early as April (in 2005) and in May of 3 years (Figure 3). The juveniles generally persisted in these collections until August with a few as late as November in some years. Juvenile persistence was not always presaged by high larval abundance in spring; thus trap collections over a protracted period could have reflected survival or longer estuarine residence rather than just gradually diminishing sample returns of a high local recruitment event. Annual variation for juveniles was as pronounced as that of larvae (Figure 4). Regression of annual juvenile CPUE on larval density explained less variance ($R^2 = 0.206$) than larvae on trawl survey biomass but was still moderate and significant ($F = 5.196$, $p = 0.034$, Figures 3 and 4).

Relationship with temperature

Regression of winter flounder larval abundance residuals against February, March, April, or May temperatures of the same year accounted for very little variation; slopes approached zero, and none of the tests were significant (Figure 5, Table 1). The ACF did not depart from random (range = -0.0213 to 0.165, 95% confidence interval $\pm$ 0.420) and so were not built into the ensuing regression model. However, residuals were not evenly distributed over the range, so the relation was complicated (Figure 5). The distribution of residuals was wide for years with cold or moderate February, March, or April temperatures and coalesced sharply at or below the mean for those years with warm temperatures (5–7°C for February, 7–9 for March, and 11–20 for May), and the fit and probability values declined progressively with each successive month (Table 1). Thus, larval recruitment corrected for stock size was uniformly low when winter/spring temperatures were warm in a given year but ranged widely if they were cold. A regression of the residuals of this relationship on temperature was based on a degree day measure and is reported below after findings of the long-term temperature analysis itself.

While the mean temperature of a spring month was always warmer in the ensuing months of the same year, the magnitude of the difference varied greatly, ranging between 0 and 8°C (Figure 5). Correlation of preceding and following months was moderate and significant for February and March ($\rho = 0.51$, $p = 0.011$) and for March and April ($\rho = 0.46$, $p = 0.025$), but not April and May ($\rho = 0.35$, $p = 0.097$) at $\alpha = 0.05$. The difference between February and March temperatures is increasing and a trend in the difference between April and May temperatures is decreasing, reflecting that water is warming earlier now than in the recent past. However, warming slowed later in the year, so that

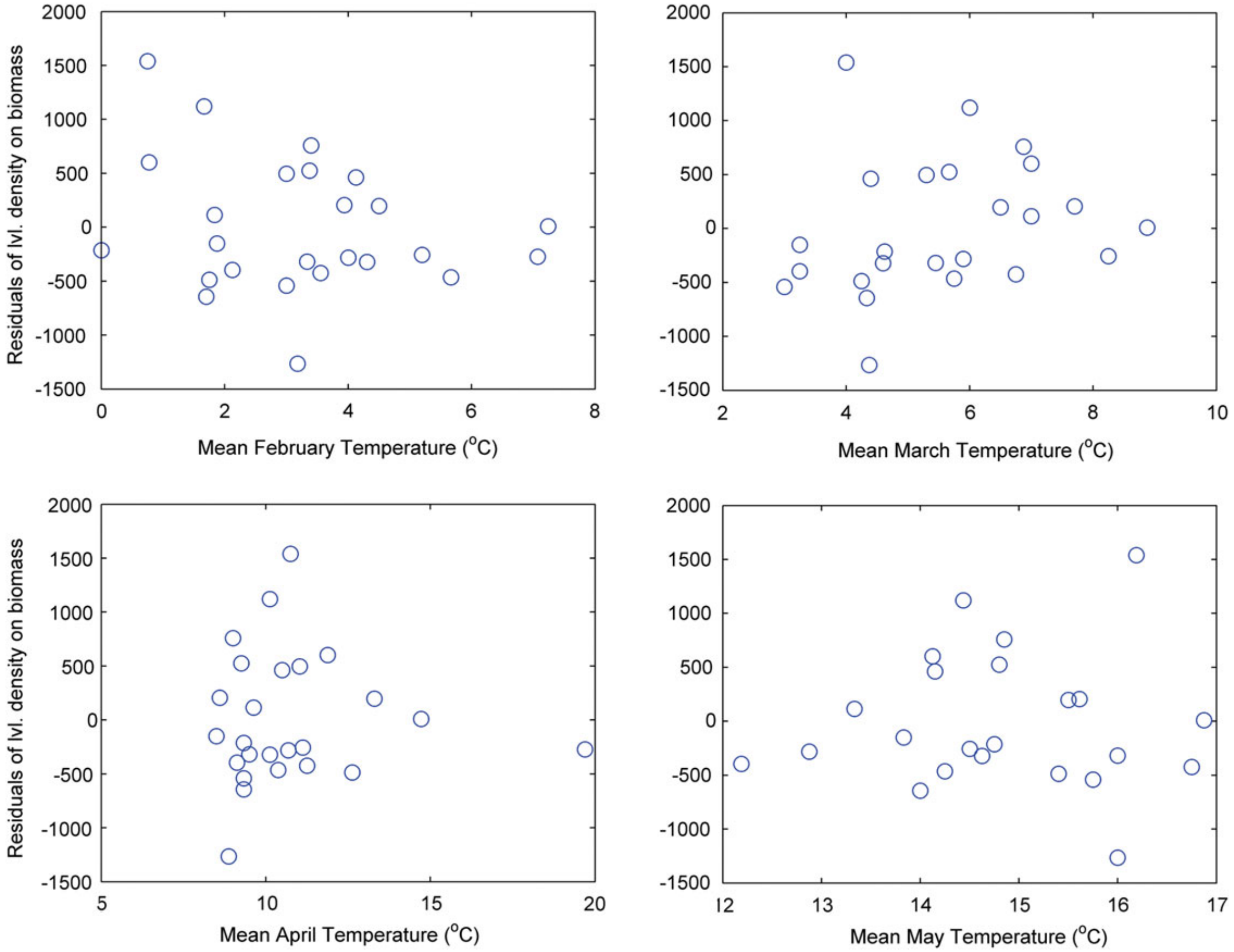

Figure 5. Scatterplot of the residual winter flounder larval density from Little Sheepshead Creek behind Little Egg Inlet (accounting for SSB effect) on annual temperature difference in the 4 months of spawning, incubation, and planktonic period from 1998 to 2012.

Table 1. Fit of regression residuals from winter flounder larval density at regression on estimate of relative adult biomass from New Jersey Department of Environmental Protection trawl survey along the coast of New Jersey from 1989 through 2013.

Month	r^2	F	P-value
February	0.058	1.417	0.246
March	0.046	1.060	0.314
April	$<$0.001	0.002	0.967
May	$<$0.001	0.008	0.929

See Figure 1 for sampling sites.

Table 2. Trends of monthly mean temperatures from 1997 to 2012 as measured during larval winter flounder sampling in Little Sheepshead Creek behind Little Egg Inlet, New Jersey.

Month	Fitted slope	r^2
January	$y = 0.034x + 1.7829$	0.041
February	$y = 0.0173x + 2.0308$	0.010
March	$y = -0.0251x + 5.2844$	0.013
April	$y = -0.0257x + 9.8847$	0.012
May	$y = 0.0269x + 14.143$	0.062
June	$y = 0.0414x + 18.6$	0.173
July	$y = 0.0062x + 22.284$	0.003
August	$y = 0.0239x + 22.746$	0.054
September	$y = 0.0519x + 20.227$	0.321
October	$y = 0.0671x + 14.605$	0.259
November	$y = 0.0246x + 9.881$	0.056
December	$y = 0.0763x + 4.3067$	0.187

See Figure 1 for sampling site.

late spring temperatures in our dataset were similar among years. In the yearly average, there was a warming trend explained by warming trends in all months except for March and April (Table 2). Together, these patterns are explained as a shift in the shape of the yearly temperature curve, with winter temperatures delayed and not as cold as previously, but vernal warming happening slightly later and faster. However, confidence in the trends is weak because variation from year to year is great (Table 2).

Progressive cumulative degree day referenced to 10°C for the 9 years with good quality spring temperature datasets was generally (except 2012) below 0°D until late May, and then quickly climbed to positive values (Figure 6a). It was also relatively cohesive in pattern (again except 2012) until mid-April, when divergence began. Cumulative degree day on 30 June was positively skewed and varied between 189.3 and 454.1°D with a mean of 281.4 and

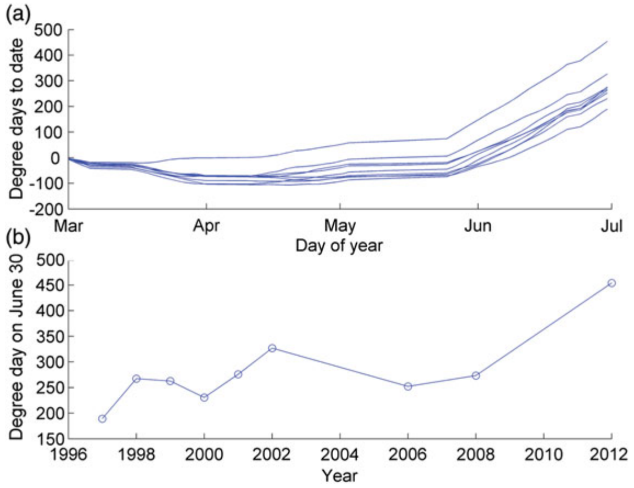

Figure 6. Dynamics of degree day (°D) relative to 10°C through the period from winter flounder spawning to juvenile settlement and growth for 9 non-consecutive years in Barnegat Bay (a). Each daily point is cumulative of all previous days in the series. Degree day for the period from 1 March to 30 June by year (b). This is the final value shown for each year in the plot above, but in chronological order.

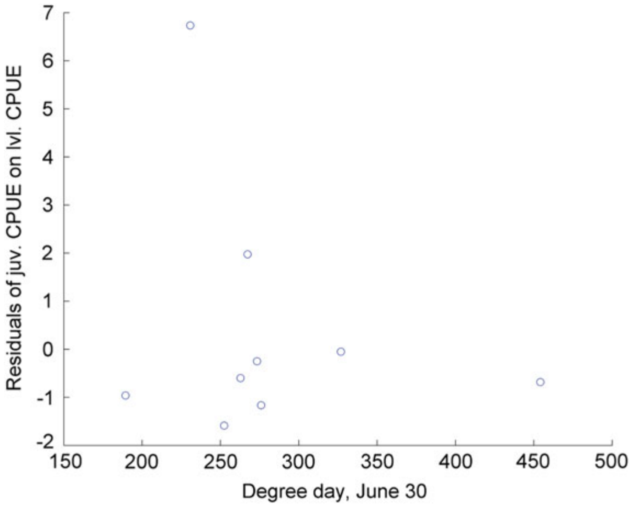

Figure 7. Scatterplot of the residuals from juvenile winter flounder abundance (CPUE) on larval density for 8 years vs. degree day (referenced to 10°C).

median 267.3°D with a general increasing trend over time, but was strongly influenced by the last year (2012, Figure 6b). Regression of the residuals of sum annual juvenile CPUE onto mean annual larval density for the 9 tested years on to degree day was random and not significant ($R^2 = 0.047$, $F = 0.347$, $p = 0.574$). However, as for larval residual recruitment on temperature, variation was great when cumulative temperature exposure was low, but at or below the expected value, when cumulative temperature exposure was great (Figure 7).

Discussion

Our work suggests that temperature increases related to climate change have not had a direct role in the historical decline of winter flounder, but a threshold effect is contributing to this decline. Our findings point to the probability of a complex temperature/recruitment relationship for winter flounder in which a secondary driver becomes important only after a critical temperature threshold is reached. This should not be tested in the same analysis. However, it is raised for further testing and is supported by an overview of the combination of literature from both field and laboratory culture experiments and is exemplified by the problem in choosing a "correct" biological reference temperature for degree day calculation. Laurence (1975) reared larval winter flounder in temperature controlled treatments of 2, 5, and 8°C, having chosen those values based on typical local estuarine temperatures in Narragansett Bay during larval recruitment during the preceding years and found that both survival and growth were significantly greater with temperature. Increased growth was observed along the coast of New Jersey, including Barnegat Bay, based on analysis of juvenile otoliths (Sogard *et al.*, 2001). Similarly, in looking for evidence of a critical period in larval development to juvenile recruitment stages, Chambers *et al.* (2001) raised winter flounder at treatments of 7, 10, 13, and 16°C, with the intention that the temperature spread would expose or exaggerate physiological vulnerability and make a critical period easier to detect. The latter two temperatures treatments are above those found naturally during spawning and early juvenile settlement, (as evidenced in this work), yet survival and growth were again progressively better with higher temperature. This is echoed in egg development (Williams, 1975). In fact, cold winters delay hatching enough to increase the probability of egg transport from shallow spawning areas to channels (Wilber *et al.*, 2013). Thus, experimental culture has not yet been undertaken at a temperature level where survival decreases, and therefore at which a realistic biological reference for degree day should be set.

It is possible, however, that warmer temperature acts indirectly on winter flounder feeding and reduced survival due to predation. Authors of rearing experiments point out the importance of the interaction of food availability with temperature in their work and the likelihood of its importance in nature. Temperature increases metabolic activity and therefore shorter times to hatching, shorter larval duration, faster growth, and higher survival, but only while it can be maintained by high feeding rates, perhaps by artificially high rates (Laurence, 1975; Chambers *et al.*, 2001). This is also echoed by modelling of winter flounder larval survival informed by laboratory values for detection, ingestion, capture efficiency, evacuation, and growth of winter flounder larvae (Beyer and Laurence, 1980). These experiments point to a possible secondary driver for the high variation at cold temperatures, i.e. when metabolic activity is low due to low temperature, food must be readily available because feeding rate is compromised. At intermediate temperatures, food may be gained even at lower concentrations through increased activity if that increased activity can be sustained. At very high temperatures, the needed food concentration may never be met in nature (Laurence, 1975; Beyer and Laurence, 1980). Finally, very warm temperatures (20–29°C) are known to inhibit feeding and reduce growth and survival of larvae and juveniles (Rogers, 1976; Keller and Klein-MacPhee, 2000; Meng *et al.*, 2000; Goldberg *et al.*, 2002) and may interact with food availability as they do at low temperatures.

Another important secondary and non-linear effect of temperature to consider is how it mediates the intersection of predator/prey phenology, but with the view of winter flounder as the prey. Regional temperature increase in spring may enhance predation on recently settled winter flounder (Taylor and Collie, 2003; Taylor and

Danila, 2005), and thus influence recruitment and subsequent year-class strength through synchronization over broad areas for winter flounder (Manderson *et al.*, 2007) and other vertebrates (Hansen *et al.*, 2013). Other factors that have a regional influence include temperature and dissolved oxygen as observed in the growth of juveniles across multiple estuaries and habitats (Phelan *et al.*, 2000). Certainly, the shift in distribution and abundance of other species in the northeastern United States is evident in response to increasing temperatures in the range of the SNE/MA winter flounder stock including for species on the continental shelf (Murawski, 1993; Pinsky and Fogarty, 2012; Richards *et al.*, 2012) and in adjacent estuaries such as Chesapeake Bay (Wood, 2000; Wingate and Secor, 2008), Narragansett Bay and Long Island Sound (Oviatt *et al.*, 2003; Oviatt, 2004; McLean, 2006; Collie *et al.*, 2008; Wood *et al.*, 2009; Howell and Auster, 2012), and the Barnegat Bay region (Able and Fahay, 2010).

Work to the north of our study site suggests that changing temperatures are likely to be the ultimate cause of the long-term decline and annual fluctuations in winter flounder abundance (Pereira *et al.*, 1999; Rock *et al.*, 2001 for review), but it is not clear what the proximal responsible mechanism(s) are.

A negative response of winter flounder to further increasing temperatures is supported by our observations of decreased larvae abundance in years with warm spring periods. Further, experiments and observations suggest a strong temperature response by winter flounder including those for experiments on muscle and nerve tissue of juveniles and adults (Battle, 1926), increasing heat stress relative to increasing size (Huntsman and Sparks, 1924), juvenile behaviour and mortality (Hoff and Westman, 1966), and overall reduced abundance (Jeffries *et al.*, 1989).

In fish and other animals with complex life histories (e.g. insects), it is clear that all life history stages (Petitgas *et al.*, 2013; Radchuk *et al.*, 2013) may contribute to the production of strong year classes and to population response to climate change (Daugherty and Smith, 2012). Based on our work, there appears a moderate influence of year-class strength of stage-specific winter flounder on the abundance of their successive stage. This is reflected at the SNE/MA stock level as well as by a significant S–R fit for SSB and age 1 recruits [Northeast Regional Stock Assessment Workshop (52nd SAW)], although that analysis uses a Beverton–Holt model over a substantially longer time-series. Interestingly, the 2013 report (un-reviewed) of the Mid-Atlantic Fishery Management Council (MAFMC) Winter Flounder Technical Committee (Report on the Federal Specifications and the Reopening of the Southern New England–Mid-Atlantic Winter Flounder Fishery, 20 May 2013) comments that "Recruits per unit stock of spawning biomass as modeled by the Beverton–Holt spawning recruit has shown marked declines during the most recent 12 years of recruitment. This suggests either a poor model fit or a change in survival due to changed conditions". They go on to use a single node regression tree model to break the S–R relationship into two phases. In contrast, the S–R fit produced by a linear model in our dataset may owe to the fact that it is entirely within a low recruitment phase and low S–R variation phase (see Duffy-Anderson *et al.*, 2005). The MAFMC report goes on to suggest that S–R modelling fit is improved by the inclusion of winter air temperature as a variate with warm winters negatively effecting recruitment. This spreads the effect of local measures over a very wide area in which substock structure is posited and likely (Sagarese and Frisk, 2011) and thus might be either completely spurious or conversely, able to detect a subtle but wide-spread effect over the noise of stronger, but highly localized drivers of recruitment success. Based on our model using local measures of abundance and temperature, we accept the null hypotheses that the remainder of the variation is not linearly related to temperature. However, we caution that this is possibly a shortcoming of the approach, in which the simplest probable relationships (in this case ordinary least-squares regression) are tested first.

Implications

We have compared our unique, long-term, annual estimates of winter flounder larvae and juvenile abundance to those for the SNE/MA stock, the southernmost of the three stocks currently identified (Pereira *et al.*, 1999; ASMFC, 2013; McBride *et al.*, 2013; McElroy *et al.*, 2013). As a result, we concur with the findings of others that climate change-induced temperature change may be influencing the decline of winter flounder but only recently, and particularly at the southern limits of its range, a process that may be common to other species (Sexton *et al.*, 2009). For this stock, the long-term collections of larvae and juveniles provide some general agreement with SSB, although the former appear to provide the best agreement. The lack of agreement between SSB at shorter timescales and individual years suggests that regional influences in temperature and perhaps other variables influence annual variation and the lack of tighter concordance between Barnegat Bay indices and the SNE-MAB stock. The same general pattern occurred for summer flounder (*Paralichthys dentatus*) using the same metrics and the same sampling programme, i.e. high estimates of SSB biomass were more likely to produce high larval abundance but not in every year (Able *et al.*, 2011).

Further, substocks within the SNE-MA stock probably exist based on morphological, genetic (Crivello *et al.*, 2004; Buckley *et al.*, 2008), tag-recapture (Phelan, 1992), and comparison of seasonal distribution and reproductive maturity data (Howe *et al.*, 1976; Pierce and Howe, 1977; Wuenschel *et al.*, 2009; McBride *et al.*, 2013). Some studies have recognized that different substocks of winter flounder may have different migration patterns and spawning locations (DeCelles and Cadrin, 2010; Sagarese and Frisk, 2011; Fairchild *et al.*, 2013). The complexity of the issue is confounded by the possibility of regional effects as has been pointed out for winter flounder metamorphoses and settlement along the coast of New Jersey at distances of 180 km (Sogard *et al.*, 2001). This small-scale regional effect has also been reported for estuaries at scales over <55–200 km in southern New England (Manderson, 2008), thus confirming the likelihood of effects at smaller scales than that of currently recognized stocks for winter flounder.

Certainly, mismatches between biological population structure and management units (Secor, 2005; Waldman, 2005; Fogarty and Botsford, 2007; Waples *et al.*, 2008; Reiss *et al.*, 2009) can confound fishery management (La Valley and Feeney, 2013). This may be especially likely for winter flounder which may have substock structure at the level of individual estuaries. To further confound the ability of managers to positively influence winter flounder abundance with harvest restrictions, the process may be less than successful if climate-induced temperature change is the dominant factor influencing population structure and abundance, especially at the southern end of the range. If this is accurate, the same may hold for other species in the Mid-Atlantic Bight. This new appreciation of climate change effects is another increase in our understanding that is enhancing our emergence from Hjort's shadow (Houde, 2008) while building on his original contributions.

Acknowledgements

Funding for this analysis was provided by the Rutgers University Marine Field Station and the New Jersey Department of Environmental Protection Barnegat Bay Program. We would also like to acknowledge all the long hours put in by many individuals to keep these time-series going, in particular: R. Hagan, D. Witting, and J. Caridad for detailed examination of larval fish collections at Little Sheepshead Creek. The NJDEP time-series in the coastal ocean was maintained by the late Don Byrne and his colleagues. The dataset was provided by Lindy Barry. This manuscript benefitted from comments by reviewers on an earlier draft. This paper is Rutgers University Institute of Marine and Coastal Sciences Contribution No. 2014–2.

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Handling editor: Howard Browman

ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2198–2207. doi:10.1093/icesjms/fst173

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment[†]

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Zwolinski, J. P., and Demer D. A. Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. – ICES Journal of Marine Science, 71: 2198–2207.

Received 4 April 2013; accepted 17 September 2013; advance access publication 18 October 2013.

We confirm that sardine recruitment in the California Current, during the last three decades, mimics aspects of the environment in the North Pacific indicated by the Pacific Decadal Oscillation (PDO) index. The periods of stock increase and decrease followed consecutive years with positive and negative PDO values, respectively. During the "warm" periods, the average number of recruits per biomass was more than threefold higher than that during the "cold" periods. In addition to the environmental conditions experienced by the sardine larvae, we show that the variability in sardine recruitment is partially explained by the environmental conditions many months before the spawning season and the adult condition factor. We hypothesize that sardine have a metabolic deficit during spawning, so prior good feeding opportunities are necessary to increase both total fecundity and offspring robustness, to enhance both reproduction and survival, respectively. Our findings augment a century-old theory that the reproductive success of small pelagic fish is governed by the survival of the early life stages. The condition of each parent also matters. To predict sardine recruitment, we propose a "dual-phase" model based on seasonal PDO-based indices and a condition factor. The model identifies summer feeding seasons conducive to a good adult condition factor followed by spring-spawning seasons supportive of good larval retention and growth.

Keywords: condition factor, environment, fecundity, prediction, spawning.

Introduction

The northern stock of Pacific sardine (*Sardinops sagax*) off the west coast of North America has exhibited multiple dramatic boom and bust cycles [see Zwolinski and Demer (2012) for two recent examples]. Although the underlying mechanisms for these cycles remain uncertain, it is broadly acknowledged that the environment plays a principal role (Jacobson and MacCall, 1995; MacCall, 2009; Zwolinski and Demer, 2012). For example, from the 1950s to the 1970s, when sardine productivity and abundance were low, the seawater temperature in the northeastern Pacific was lower than in the previous and subsequent decades (MacCall, 1979; Barnes *et al.*, 1992). This observation lead Jacobson and MacCall (1995) to model the reproductive success of sardine vs. sea surface temperature (SST) in the main sardine spawning area. For practical reasons, the modelled temperature was then indexed to the long-term time-series of SST measured at Scripps Institution of Oceanography (SIO) pier and provided a foundation for the first environmentally driven decision rule for the exploitable fraction of a fish population

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[†] This article does not necessarily reflect the official views or policies of the National Marine Fisheries Service, the National Oceanic and Atmospheric Administration, the Department of Commerce, or the Administration.

(PFMC, 1998). The aim was to reduce fishing pressure during years of low productivity and increase it during years of surplus production. However, from 2006 to 2012, despite the high SST values measured at the SIO pier, there were successive recruitment failures, fishing continued, and the stock biomass dropped to the lowest level in the most recent two decades (Zwolinski and Demer, 2012).

McClatchie *et al.* (2010) re-evaluated Jacobson and MacCall's (1995) SST-to-recruitment relationship and concluded that SST measured at the SIO pier and recruitment success (number of recruits per unit of parental biomass) were no longer correlated. They also noted a disconnection between the temperature measured at the SIO pier and that of the major sardine spawning grounds. These differences may explain why other studies have provided evidence of strong correlation between the assessed sardine recruitment and the seawater temperatures offshore (e.g. Galindo-Cortes *et al.*, 2010; Lindegren and Checkley, 2013). More generally, many other studies have shown that fluctuations in atmospheric and oceanographic conditions matched, in both period and phase, oscillations in small pelagic fish biomasses in the California Current and elsewhere (Jacobson *et al.*, 2001; Peterson and Schwing, 2003; King, 2005; MacCall *et al.*, 2005; Norton and Mason, 2005; Wells *et al.*, 2006; Deyoung *et al.*, 2008; Alheit and Bakun, 2010; Overland *et al.*, 2010; Perry *et al.*, 2010; Irvine and Fukuwaka, 2011). Therefore, it appears that environmental dynamics do affect the productivity and community structure of marine organisms, particularly small coastal pelagic fish species (CPS; Fréon *et al.*, 2005; Alheit and Bakun, 2010; Zwolinski and Demer, 2012), and the challenge is to identify the mechanisms.

Mantua *et al.* (1997) introduced the Pacific Decadal Oscillation (PDO), an index that tracks a pattern in the SST of the north Pacific that fluctuates at multidecadal scales and which describes environmental dynamics that have profound effects on the recruitment and biomass of certain salmon stocks in Alaska. The environmental dynamics reflected by the PDO were also related to the total biomass and diversity of copepods off northern California (CA) and Oregon (OR), which in turn have strong impacts on the local salmon recruitment (Peterson and Schwing, 2003). Concurrently, Chavez *et al.* (2003) analysed low-frequency oscillations in CPS abundances in the 20th century and concluded that cold periods off the west coast of the United States, implicitly described by the PDO, were coincident with decades of anchovy dominance. Conversely, warm periods, also indicated by a positive PDO, were associated with decades of sardine dominance. Chavez *et al.* (2003) noted that the principal characteristics of the multidecadal "sardine regimes" in the northeastern Pacific were: warmer than average SST, strong stratification, low nutrients in the photic layer, and low overall productivity, and more frequent *El Niño* Southern Oscillation (ENSO) episodes. They also suggested pathways through which the environment could affect the epipelagic community.

Rykaczewski and Checkley (2008) advanced a mechanistic approach to hindcast surplus sardine production. They showed that sardine surplus production, which is directly related to reproductive success, is significantly correlated with the intensity of curl-driven upwelling offshore of southern CA during spring and summer (May–July). Their work supports a century old theory that the survival of early life stages, mediated by their environment, controls recruitment success for sardine and other CPS (Hjort, 1914; Cury and Roy, 1989; Cury *et al.*, 2000). However, Zwolinski and Demer (2012) found that the condition factor of adult sardine, which is an indicator of their forthcoming total fecundity (Marshall *et al.*, 1999), may also help to predict recruitment. Their observation emphasized the importance of parental condition to successful reproduction via both increased fecundity and more robust and resilient offspring (Riveiro *et al.*, 2004; Garrido *et al.*, 2008). Mechanistically, sardine tend to rely principally on fats and proteins stored prior the spawning season to provide energy for the protracted energy expenditure (Ganias *et al.*, 2007).

Lindegren and Checkley (2013) updated the analyses done by Jacobson and MacCall (1995) and McClatchie *et al.* (2010) and found that the spring and annual averages of the SST measured offshore during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys during the spawning year are explanatory variables for sardine recruitment and the recruitment-to-parental biomass ratio. However, in their analysis the larger scale multivariate ENSO and PDO indices did not perform as well as the regional offshore temperature.

To explain why the local environmental indices out-performed the large-scale indices, we hypothesize here that the reproductive success of sardine is determined by a sequence of environmental conditions initiated many months before the spawning season, continuing through the larval period. If correct, then environmental indicators for feeding conditions during summer, and those for larval retention and growth the following spring, should collectively predict recruitment. In this paper, we propose such a "dual-phase" environmental indicator, based on the averages of the monthly PDO index, which may predict sardine recruitment.

Methods

To investigate the environmental drivers of sardine recruitment, we first explored the correlation between the logarithmic reproductive success (the logarithm of the number of recruits per unit of spawning biomass; Jacobson and MacCall, 1995) and each of three large-scale indices and one regional oceanographic index. We then fit a formal stock–recruitment model, allowing for environmental dependence (Jacobson and MacCall, 1995). Using the best model, we reconstructed the time-series of sardine recruitment in the 20th and 21st centuries, for years with available estimates of biomass. Finally, we included the adult condition factor in the environmental stock–recruitment model and evaluated its relative performance. The adult condition factor may control the reproductive output and thereby the recruitment success (Zwolinski and Demer, 2012). The data and modelling procedures are explained in detail below.

Recruitment and biomass data

Using the results of the 2010 stock assessment model (Hill *et al.*, 2010), recruitment (R) was estimated by the abundance of age-0 sardine in July, and the parental stock of sardine (S) was estimated by the biomass of age-1 and older (age-1+) sardine in January of the same year, from 1981 to 2011. We used the 2010 assessment model because its results, or results from earlier models with the same configuration, have been used previously to evaluate the dependence of sardine recruitment on the environment (Galindo-Cortes *et al.*, 2010; McClatchie *et al.*, 2010; Lindegren and Checkley, 2013).

Condition factor data

Currently, the majority of the sardine spawning population migrates seasonally to feed during summer and autumn in the productive areas off OR, WA, and VI (Zwolinski *et al.*, 2011; Demer *et al.*, 2012). These migrations appear to allow sardine to store fat for use during the subsequent reproductive season. The condition factor [k; $k = 10^5 \times$ body weight (g)/standard length^3 (cm)], related to the amount of body fat, may be a proxy for reproductive output and thus sardine recruitment (Zwolinski and Demer, 2012). For the period 1999–2007, values of k for the migrating portion of the stock were estimated from the OR and Washington (WA) fishery statistics. The average k values for each year were estimated from predominantly adult sardine (standard length, SL, $\geq$160 mm) landed there between August and October before each recruitment year.

Environmental data

We used three remotely-sensed large-scale environmental indices evaluated monthly: the multivariate *El Niño* index (MEI; http://www.esrl.noaa.gov/psd/enso/mei/table.html; Wolter and Timlin, 1998); the PDO (http://jisao.washington.edu/pdo/PDO.latest; Mantua *et al.*, 1997); and the North Pacific Gyre Oscillation (NPGO; http://www.o3d.org/npgo/npgo.php; Di Lorenzo *et al.*, 2008). These three variables were selected based on previous recognition of their ability to summarize multiple oceanographic variables in the northeast Pacific that are relevant to the dynamics of CPS (Mantua *et al.*, 1997; Peterson and Schwing, 2003; Di Lorenzo *et al.*, 2008; King *et al.*, 2011). To represent the environmental conditions encountered by adult sardine during their summer feeding season, we averaged these indices during summer (August through October) before the spawning season. To represent the environmental conditions experienced by the early life-stages, we averaged the indices during spring (March through July) of the spawning (and recruitment) year. To represent the environmental conditions experience by the adult and early life-stage sardine, we summed the two seasonal PDO indices.

Although we aimed to investigate any relationships between these indices of large-scale oceanographic phenomenon and sardine recruitment, we also analysed, for completeness, the regional temperature-based indices from Lindegren and Checkley (2013). These indices were computed from seawater temperature averaged from 5 to 15 m depth during the spring CalCOFI surveys ($\text{SST}_{\text{spring}}$) and during the four (winter, spring, summer, and fall) CalCOFI surveys ($\text{SST}_{\text{annual}}$).

Modelling approach

We first explored the correlation between the logarithmic recruitment success [$\log(R/S)$] and the selected environmental variables using the Pearson linear correlation analysis. This exploratory analysis quantifies the covariability between the multiple variables and thereby guides subsequent model fitting.

We fit a variant of the linearized Ricker R–S relationship (Quinn and Deriso, 1999), as implemented by Hill *et al.* (2011), but with the addition of environmental variables potentially related to recruitment, as in Jacobson and MacCall (1995). The data were fit to the following generalized linear model:

$$\log(\bar{R}) = \text{offset}(\log(S)) + \beta_0 + \beta_1 S + \sum_{j=1}^{J} \beta_{j+1} I_j, \qquad (1)$$

where $\bar{R}$ is the expected value of recruitment in million of fish, offset($\log(S)$) the logarithm of the age-1+ biomass with a fixed coefficient of 1 (McCullagh and Nelder, 1989), β_0 the intercept, β_1 the slope parameter for the S; and the j environmental indices I_j have respective coefficients β_{j+1}. In Equation (1), error is evaluated only in the recruitment, allowing the use of many error structures for positive data, including the frequently used lognormal distribution (McCullagh and Nelder, 1989). The model was fit via a stepwise forward and backward selection procedure beginning with the S term, followed by the environmental variables with highest correlation with $\log(R/S)$. The model fit was evaluated with plots of the residuals to check for the homogeneity of the variance and independence of the residuals (McCullagh and Nelder, 1989). Contingent on the fit of the model, forward inclusion of the variables was tested via the Akaike Information Criterion (AIC), which is an index that summarizes the quality of the fit and the parsimony of the model (Hobbs and Hilborn, 2006). To obtain a measure of global goodness of fit, we computed the square of the correlation coefficient between the logarithms of the fitted values and the logarithms of the observations. In a linear or additive model with a lognormal response, this quantity, named here as the "R^2 equivalent," corresponds to the unadjusted R^2 statistic and to the percentage of deviance explained by the model. The models were fit using the library mgcv for R (Wood, 2006).

The predictive performance and the stability of the fitted models were assessed by cross-validation. For each of 1000 repetitions, three-quarters of the data were randomly selected (the training set) and used to fit the recruitment model; the model was used to predict the recruitment for the remaining quarter of the data (testing set). The R^2 equivalent of the training and testing sets were recorded, as well as the AIC of the training set. Model overfitting is suspected if the R^2 equivalent of the testing set is much less than that for the training set.

Because k, which is a proxy for total fecundity, depends significantly on whether the stock migrates north during summer to feed, the environmental Ricker model [Equation (1)] was fit with k only for the period when the stock is known to have undergone feeding migrations, i.e. for the period from 1999 to 2008. Including k in the best environmental Ricker model requires the model to be fitted with two extra parameters: one is a binary variable indicating whether k exists (i.e. pre- or post-1999), and the second is the slope relative to k, conditioned on k being available.

Results

Environmental indices and sardine reproductive success

Statistically significant correlations were found between $\log(R/S)$ and each of the large-scale environmental indices, averaged during summer before the spawning season and during spring of the spawning and recruitment year (Figure 1, Table 1). The strongest correlation with a large-scale seasonal index was between the PDO during summer before the spawning season ($\text{PDO}_{\text{summer}}$), followed by the PDO during the subsequent spring ($\text{PDO}_{\text{spring}}$). The correlation was highest for the summed $\text{PDO}_{\text{summer}}$ and $\text{PDO}_{\text{spring}}$ indices ($\text{PDO}_{\text{combined}}$). The temperature indices for the southern California region were also significantly correlated with $\log(R/S)$, but less than with $\text{PDO}_{\text{summer}}$ and $\text{PDO}_{\text{combined}}$ (Table 1). The various environmental variables are also significantly cross-correlated (Figure 1, Table 1), which reaffirms the known connections between them (Wells *et al.*, 2006).

Regression analysis

Without environmental indices, Equation (1) is a biomass-only model. In this case, β_1 is highly significant and has a negative slope, indicating a strong compensation of parental biomass on recruitment (Table 2, Figure 2). Based on its high linear correlation coefficient, $\text{PDO}_{\text{combined}}$ was the first environmental variable to be included in the model. It significantly reduced the unexplained variance of the biomass-only model and the residuals were homogeneously distributed with no signs of autocorrelation. Recruitment compensation was also reduced considerably (Table 2, Figure 2), but remained significant. Additional large- and regional-scale variables did not improve the model fit sufficiently to warrant their inclusion in the model. This is likely because the indices contain redundant information, as indicated by their high cross-correlations (Table 1). However, when tested in isolation, all the large-scale environmental indices proved to significantly reduce the proportion of unexplained

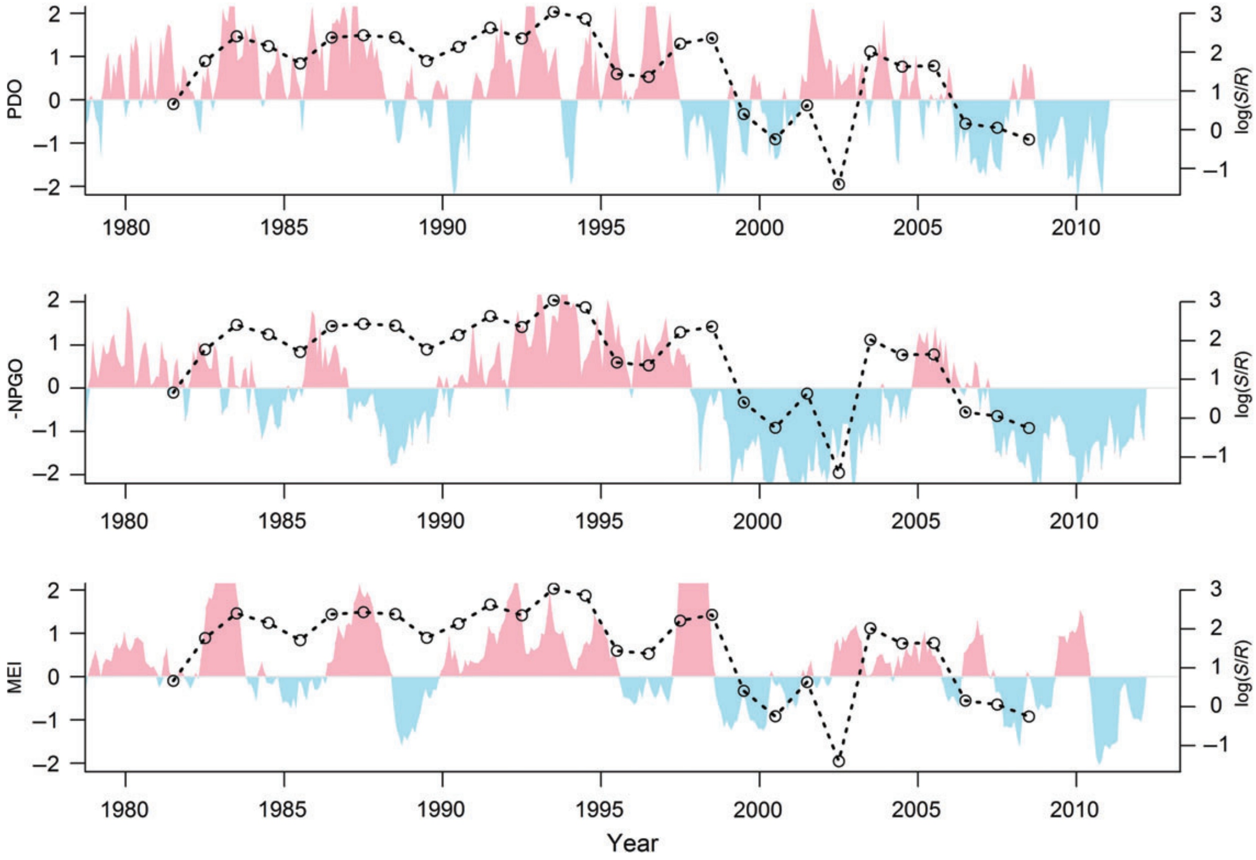

Figure 1. Logarithmic reproductive success (dashed line) from the 2010 assessment (Hill *et al.*, 2010), overlaid on the monthly values of large-scale oceanographic monthly PDO index; North Pacific Gyre Oscillation index (NPGO); and Multivariate ENSO Index (MEI).

Table 1. Correlation matrix (*r*- and *p*-values) between the environmental indices, biomass of sardine age-1 and older (*S*), and logarithmic recruitment success [log(*R*/*S*)].

r ***p*-value**	**S**	**log(*R*/*S*)**	**PDO$_{\mathrm{spring}}$**	**PDO$_{\mathrm{summer}}$**	**MEI$_{\mathrm{spring}}$**	**MEI$_{\mathrm{summer}}$**	**NPGO$_{\mathrm{spring}}$**	**NPGO$_{\mathrm{summer}}$**	**SST$_{\mathrm{annual}}$**	**SST$_{\mathrm{spring}}$**	**PDO$_{\mathrm{combined}}$**
S	*****	−0.663	−0.395	−0.512	−0.316	−0.22	0.467	0.394	−0.364	−0.571	−0.538
log(R/S)	<0.001	*****	0.537	0.673	0.53	0.43	−0.503	−0.49	0.62	0.531	0.718
PDO$_{\mathrm{spring}}$	0.038	0.003	*****	0.424	0.618	0.496	−0.576	−0.61	0.691	0.592	0.841
PDO$_{\mathrm{summer}}$	0.005	<0.001	0.025	*****	0.271	0.613	−0.309	−0.542	0.437	0.407	0.847
MEI$_{\mathrm{spring}}$	0.102	0.004	<0.001	0.163	*****	0.582	−0.499	−0.505	0.671	0.619	0.525
MEI$_{\mathrm{summer}}$	0.26	0.022	0.007	0.001	0.001	*****	−0.214	−0.512	0.531	0.368	0.658
NPGO$_{\mathrm{spring}}$	0.012	0.006	0.001	0.109	0.007	0.275	*****	0.742	−0.338	−0.566	−0.523
NPGO$_{\mathrm{summer}}$	0.038	0.008	0.001	0.003	0.006	0.005	<0.001	*****	−0.508	−0.485	−0.682
SST$_{\mathrm{annual}}$	0.057	<0.001	<0.001	0.02	<0.001	0.004	0.079	0.006	*****	0.615	0.667
SST$_{\mathrm{spring}}$	0.001	0.004	0.001	0.032	<0.001	0.054	0.002	0.009	<0.001	*****	0.591
PDO$_{\mathrm{combined}}$	0.003	<0.001	<0.001	<0.001	0.004	<0.001	0.004	<0.001	<0.001	0.001	*****

Spring indices are monthly averages from March through July of the recruitment year. Summer indices are monthly averages from July through October of the year before recruitment. Note the strong correlation between all environmental variables for each season, and the relative independence between the PDO$_{\mathrm{summer}}$ and the NPGO$_{\mathrm{spring}}$ and MEI$_{\mathrm{spring}}$. See Wells *et al.* (2006) for related analysis and discussion.

variance in recruitment in relation to the model using only the biomass as the predictor (Table 2). The models fit with the regional SST indices also explained large proportions of the recruitment variability (Table 2). However, they were more prone to overfitting than those using PDO$_{\mathrm{summer}}$ or PDO$_{\mathrm{combined}}$ (Table 3).

The model using the PDO$_{\mathrm{combined}}$:

$$\bar{R} = \exp(-4.194) \times S \times \exp(-8.511 \times 10^{-7} S + 0.267\,\mathrm{PDO}_{\mathrm{combined}}) \tag{2}$$

had the highest proportion of the variance explained (for both the training and testing sets; Table 3), low AIC (Tables 2, 3), and independently distributed residuals. The global fit is very satisfactory and the R^2 equivalent is 0.85.

The three highest recruitments occurred during 1997, 1998, and 2003 when the sardine biomass was in the mid-range, i.e. ca. 750 000 tonnes (Figure 2). Below this optimal biomass value sardine production decreased quasi-linearly with biomass. Above this value, the parental biomass compensation effect forced recruitment into a plateau or decline (Figure 2). The shape of the curve does not change significantly vs. the environmental index, but its scaling is extremely variable. For example, 1998 and 2002 had similar biomasses but the observed recruitments differed by 25-fold and the corresponding environmentally induced variations in the fitted model were 3.5 times higher than that of the lowest estimate (Figure 2).

Table 2. Summary statistics for a subset of the evaluated environmental Ricker models [Equation (1)].

Explanatory variables	Linear coefficients	AIC	R^2 equivalent
S	$-1.135e^{-06}$	501.8	77.1
$S + \mathrm{MEI}_{\mathrm{summer}}$	$-1.056e^{-06}$, $3.367e^{-01}$	498.3	80.7
$S + \mathrm{MEI}_{\mathrm{spring}}$	$-9.616e^{-07}$, $4.743e^{-01}$	494.9	81.8
$S + \mathrm{NPGO}_{\mathrm{summer}}$	$-9.098e^{-07}$, $-2.595e^{-01}$	500.3	79.1
$S + \mathrm{NPGO}_{\mathrm{spring}}$	$-9.277e^{-07}$, $-2.145e^{-01}$	501.1	78.6
$S + \mathrm{PDO}_{\mathrm{spring}}$	$-1.033e^{-06}$, $3.098e^{-01}$	499.3	81.6
$S + \mathrm{PDO}_{\mathrm{summer}}$	$-8.285e^{-07}$, $4.346e^{-01}$	495.9	83.3
$S + \mathrm{SST}_{\mathrm{spring}}$	$-9.384e^{-07}$, $3.261e^{-01}$	499.6	79.1
$S + \mathrm{SST}_{\mathrm{annual}}$	$-9.119e^{-07}$, $6.984e^{-01}$	491.9	84.2
$S + \mathrm{PDO}_{\mathrm{combined}}$	$-8.511e^{-07}$, $2.665e^{-01}$	492.1	85.1
$\mathrm{PDO}_{\mathrm{combined}}$	$3.469e^{-01}$	500.7	79.7

S is the parental biomass. The models were fitted using a logarithmic link function with a negative binomial distribution, with theta estimated during the fitting procedure. The linear coefficients represent the fitted parameters for the predictor variables. AIC is the Akaike Information Criterion. R^2 equivalent is the square of the coefficient of correlation between the logarithm of the observed recruitment and the logarithm of the fitted ones. None of the model residuals were autocorrelated. All model parameters were significant for $\alpha = 0.1$ or lower. The number of observations is 28.

Because k, a proxy for total fecundity, depends significantly on whether the stock migrates north during summer to feed, the environmental Ricker model was fit without k for the period from 1981 through 1998 [Equation (3a)] and with k for the period from 1999 to 2011 [Equation (3b)]:

Table 3. Cross-validation results for a subset of the models tested.

Explanatory variables	Training median AIC	Training median R^2 equivalent	Testing median R^2 equivalent
S	375.1	76.7	82.1
$S + \mathrm{MEI}_{\mathrm{summer}}$	372.9	80.4	84.0
$S + \mathrm{MEI}_{\mathrm{spring}}$	370.2	80.9	86.8
$S + \mathrm{NPGO}_{\mathrm{summer}}$	374.2	79.5	79.4
$S + \mathrm{NPGO}_{\mathrm{spring}}$	374.9	78.6	78.5
$S + \mathrm{PDO}_{\mathrm{spring}}$	373.3	82.5	81.6
$S + \mathrm{PDO}_{\mathrm{summer}}$	371.8	83.6	84.3
$S + \mathrm{SST}_{\mathrm{spring}}$	375.4	79.0	81.6
$S + \mathrm{SST}_{\mathrm{annual}}$	369.3	84.9	81.6
$S + \mathrm{PDO}_{\mathrm{combined}}$	368.8	85.6	84.6
$\mathrm{PDO}_{\mathrm{combined}}$	375.0	78.9	79.1

The 2003 and 1998 recruitments, which produced large residuals in the fitted models, were more often selected to the training vs. testing set and caused the median R^2 equivalent of the testing sets to be higher than that of the training sets in some of the fitted models.

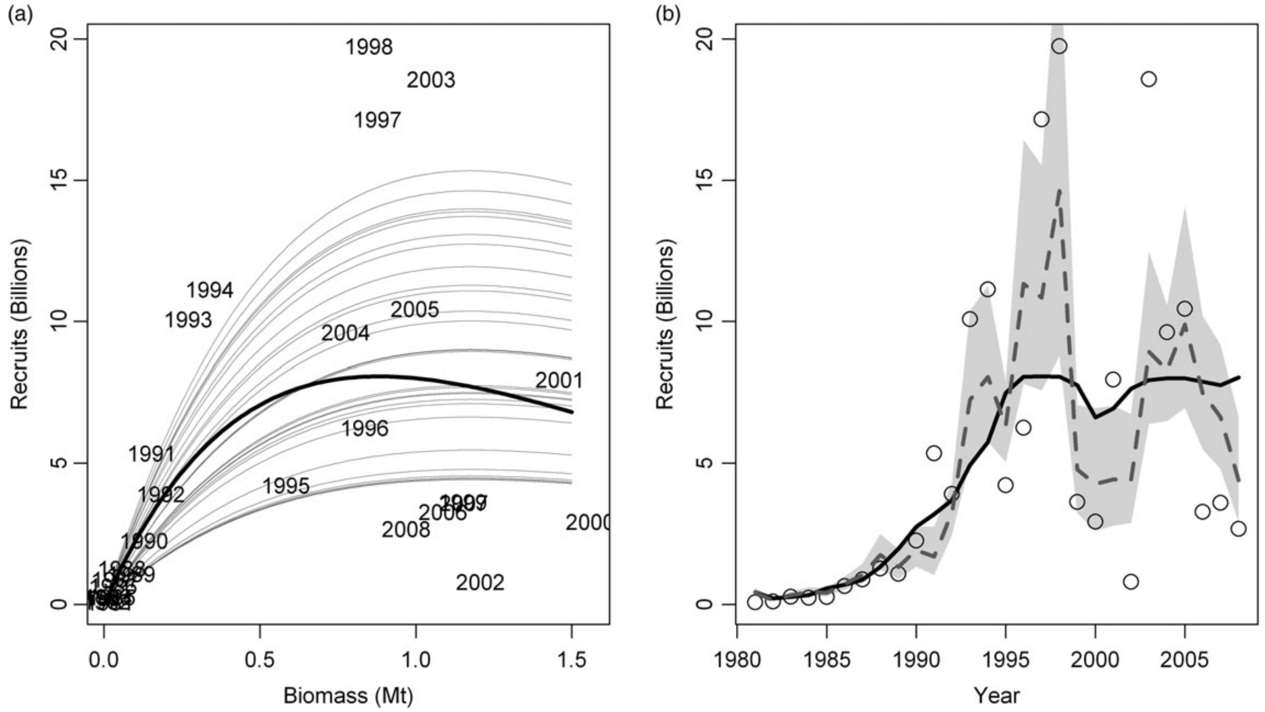

Figure 2. (a) Environmental Ricker model (grey, corresponding to 1 line per year) vs. the static Ricker model (black), and (b) reconstruction of the recruitment time-series for the sardine stock from 1981 to 2008 (circles) using the static model (black) and environmental Ricker model (dashed grey) corresponding to the best model [Equation (2); Table 2], with 95% confidence intervals for predicted recruitment (grey area).

$$\bar{R} = \exp(-4.137) \times S \times \exp(-8.079 \times 10^{-7}S + 0.234\text{PDO}_{\text{combined}}), \tag{3a}$$

$$\bar{R} = \exp(-11.826) \times S \times \exp(-8.079 \times 10^{-7}S + 0.234\text{PDO}_{\text{combined}} + 4.71k). \tag{3b}$$

The coefficient for *k* is positive and statistically significant ($p < 0.1$). The model including *k* [Equations (3a) and (3b)] has a higher R^2 equivalent (86.2) and lower AIC (492.0) relative to the best model in Table 2, and the residuals for the 1999–2011 period are smaller (Figure 3).

Discussion

All the models tested showed that environmental dynamics in the northeastern Pacific, particularly well captured by the PDO, significantly influenced sardine recruitment. Although sardine recruitment is strongly linked to the dynamics of their environment (e.g. Barnes *et al.*, 1992; Jacobson and MacCall, 1995; Jacobson *et al.*, 2001; MacCall, 2009; Zwolinski and Demer, 2012; this work), most studies assumed that sardine recruitment is predicated on the environment relevant to early (eggs and larvae) and juvenile life stages (Hjort, 1914; Lasker, 1981; MacCall, 2009; pers. comm. Rykaczewski and Checkley, 2008; McClatchie *et al.*, 2010; Lindegren and Checkley, 2013). For example, Lasker (1981) hypothesized that larval survival depends on the stability of the environment and the quality (species composition and size) and density of their food. MacCall (2004) associated large sardine recruitments to the retention of larvae in the nursery grounds, which is maximized during low flows of the California Current. Also, Rykaczewski and Checkley (2008) observed that zooplankton size was related to the intensity of curl-driven upwelling offshore of southern California, which was correlated with surplus sardine production. Considered together, these findings relate strong sardine reproductive success (large recruitment) via larval survival to SSTs (Galindo-Cortes *et al.*, 2010; Lindegren and Checkley, 2013), the strength of the California Current (MacCall, 2009), and upwelling patterns (Rykaczewski and Checkley, 2008). To our minds, these characteristics recount complementary manifestations of the same basin-scale oceanographic phenomena that affect the dynamics of the biotic and abiotic environment in the California Current (Mantua *et al.*, 1997; Peterson and Schwing, 2003; Wells *et al.*, 2006; Keister *et al.*, 2011; Macias *et al.*, 2011) and that are indicated by positive PDO and *El Niño* indices (Macias *et al.*, 2011, 2012).

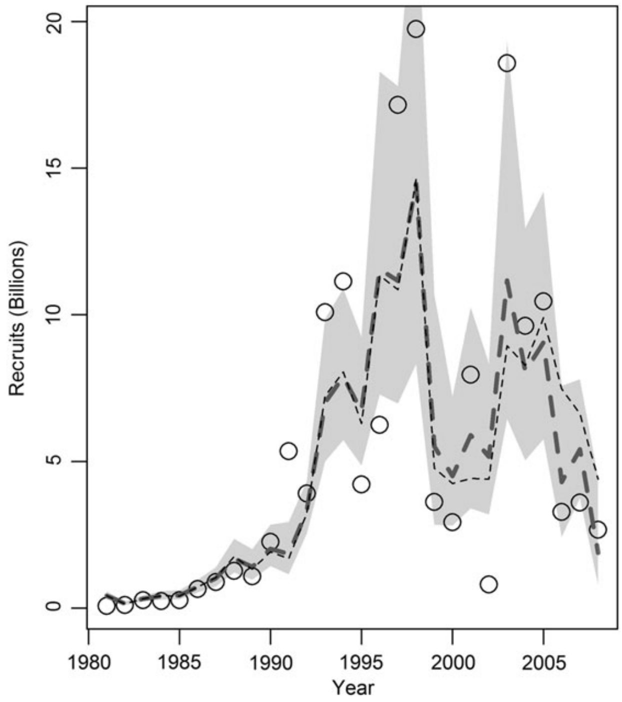

Figure 3. Reconstruction of the recruitment time-series for the sardine stock from 1981 to 2008 (circles) using the best environmental Ricker model [Equation (2); Table 2; black dashed line]; and the best environmental Ricker model with *k* [Equation (3); grey dashed line] with 95% confidence intervals (grey area). The inclusion of *k* provides a better fit to the data after 2000.

Although the survival of sardine larvae and juveniles is controlled by the physical environment (Cury *et al.*, 2000; Bakun, 2010), the availability of quality prey (Hjort, 1914), and predation and cannibalism for eggs and larvae (Ricker, 1954; Pitcher and Hart, 1982), we found that the highest correlations between sardine recruitment and the PDO-based index occur before the spawning season. Therefore, sardine recruitment appears to be not only related to the environment of the early life stages, but also to the cumulative effect of the environment on the adult sardine before spawning.

Sardine, perhaps more so than anchovy and other CPS, are "capital breeders", i.e. their reproduction depends mainly on stored reserves, so parental condition may be vital for sustained reproductive effort (Kawasaki and Omori, 1995). Sardine spawning generally occurs after the period of highest fat accumulation (Zwolinski *et al.*, 2001; Garrido *et al.*, 2007). To spawn throughout a protracted season, with limited food ingestion, sardine depend greatly on the storage of high-energy lipids (Zwolinski *et al.*, 2001; Garrido *et al.*, 2007). The relationships between body fat quality and quantity and recruitment success are not well characterized nor perhaps broadly appreciated for sardine, but a significant positive correlation between the condition factor (i.e. body mass per cubic unit length) or lipid content and recruitment success were found for Pacific sardine in the California Current (Zwolinski and Demer, 2012) and Japan (Kawasaki and Omori, 1995), and European sardine (*Sardine pilchardus*; Rosa *et al.*, 2010). Zwolinski and Demer (2012) showed that *k* is positively correlated with recruitment, irrespective of the conditions necessary for larval and juvenile survival. Here, we showed that the *k* for migrating fish has a significant role on the prediction of sardine recruitment, supporting the expectation that the migration provides metabolic advantages. As previously shown for gadoids (Marshall *et al.*, 1999) and suggested for sardine (Kawasaki and Omori, 1995), the storage of fats in advance of the spawning season translates into increased fecundity, more resilient offspring, and potentially increased recruitment.

The statistically significant covariation between recruitment and the PDO during summer preceding the spring spawning is somewhat independent of the sardine biomass and condition factor. A potential explanation for why the environment before spawning might affect recruitment, irrespective of the condition factor (driven exclusively by weight changes), may be related to quality vs. quantity of their food. Oocyte formation requires not only fat but also proteins for structural components. These are known to depend on body tissue composition, which in turn depends on the biochemical contents of the prey (Riveiro *et al.*, 2004; Bode *et al.*, 2007; Garrido *et al.*, 2008). In the California Current, perhaps the prey cascade resulting from a changing environment (Peterson and Schwing, 2003; Keister *et al.*, 2011) could vary the biochemical composition of oocytes and affect their survival. Alternatively, "preconditioning", described by Schroeder *et al.* (2013), may explain how basin-scale oceanographic indices (e.g. $\text{PDO}_{\text{summer}}$) predict regional near-term phenomena (e.g. spring-spawning success). These two hypotheses may be complementary and should be tested for sardine in the California Current.

Despite the strong relationship we found between the PDO-based index and assessment-based estimates of sardine-stock recruitment, the latter may be compromised by an incomplete separation of the northern and southern stocks in the landings data (Jacobson and MacCall, 1995; Félix-Uraga *et al.*, 2005; Demer and Zwolinski, 2013). In particular, because the fisheries off Ensenada, Mexico, and San Pedro, CA, likely exploit two stocks (Félix-Uraga *et al.*, 2004, 2005; Demer and Zwolinski, 2013), the use of combined northern and southern stock landings in the assessment may have caused anomalously strong (e.g. 2003) or weak (e.g. 2002) estimates of recruitment that were not as evident in the survey time-series (Zwolinski *et al.*, 2012; Demer *et al.*, 2013; Zwolinski and Demer, 2013). Therefore, the recruitment time-series should be re-estimated with environmentally dependent stock partitioning (Demer and Zwolinski, 2013), and then this analysis should be revised. Improved accuracy in the estimated recruitment time-series could strengthen the performances of our models.

Notwithstanding the need to better differentiate the sardine stocks before an accurate evaluation of sardine recruitment (Félix-Uraga *et al.*, 2005; Hill *et al.*, 2006; Demer *et al.*, 2013; Demer and Zwolinski, 2013), periods of stock expansion and contraction in the 20th and 21st centuries are well explained by the environmental conditions indicated by the PDO (Chavez *et al.*, 2003; Zwolinski and Demer, 2012; Deyle *et al.*, 2013). Although McClatchie (2012) did not find significant relationships between the PDO and sardine abundance on a longer time-scale, this may be due to uncertainty and noise in the data used to approximate the PDO (tree rings) and sardine abundance (fish-scale deposition), excessive smoothing of the data, or both.

The principal merits of using the PDO, vs. a small-scale index or survey-based measurements (e.g. the CalCOFI temperature index), is that it conveys sufficient information pertaining to the processes that were identified to directly affect recruitment (Lasker, 1981; Rykaczewski and Checkley, 2008; Chavez *et al.*, 2003) and it is readily and continuously available. Furthermore, from an operational standpoint, annually integrated survey-based metrics of the regional environment may require resources that could be directed to the sampling of the entire adult population. Finally, seasonal indices, as opposed to multiyear average indices, are better predictors of recruitment, because recruitment expectations are independent from the past year's environment or average condition factor.

If the best stock recruitment model [Equation (2); Table 1] approximates reality, then the sardine abundance over the last century is governed by the cumulative effect of the annual recruitment success permitted by environmental conditions indicated by the PDO (Figure 4). Positive PDOs were correlated with large sardine recruitment, and consequentially biomass surpluses. Therefore, predominantly positive PDO periods (1920–1930s and 1980–1990s) were related to cumulatively larger sardine biomasses. Conversely, during prolonged periods with negative PDO values (1950–1970s and 2006 to the present), the reproductive success was low, and with total mortality exceeding recruitment, the population declined (Parrish, 2000; Zwolinski and Demer, 2012). More

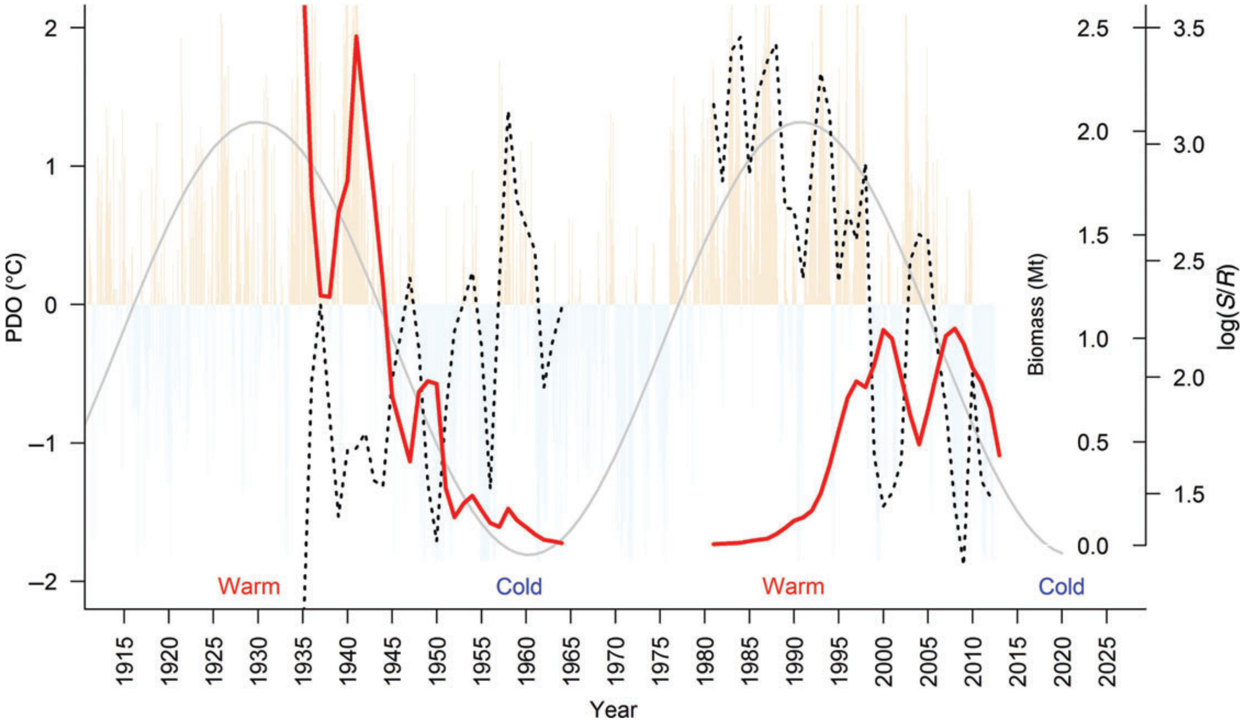

Figure 4. The PDO index indicating positive (pink) and negative (light blue) monthly values; the 60-year periodic component of the PDO projected to 2020 (grey line; Zwolinski and Demer, 2012); the assessment estimated sardine biomass (red); and the predicted logarithmic stock–recruitment ratio (dashed line).

specifically, the decline in the sardine stock around 1935 resulted from low recruitment success due to high biomasses, in conjunction with high exploitation (Radovich, 1982; Parrish, 2000; Zwolinski and Demer, 2012). During the mid-1940s, the PDO locked into a negative phase, high exploitation continued, and the stock plummeted. During the next three decades, the PDO was largely negative, the reproductive success of sardine was low and sardine continued to decline until they were virtually absent from all of their historical fishing grounds and their biomass was untraceable (Parrish, 2000).

Only in the 1980s, when the PDO became mainly positive again and fishing mortalities were low (Hill *et al.,* 2010), the population recovered at a rate of as much as 30% per year (Figure 4). The direct effect of the environment on the dynamics of the stock can be seen in the rapid decline in the biomass from 1999 through 2003, in agreement with 4 years of negative PDO values. The rate of decrease, 16% per year, is higher than the exploitation rate (∼11% per year; Hill *et al*., 2010), so recruitments were less than total mortality, even in the absence fishing. Three strong year classes (2003–2005) contributed to a temporary resurgence of the stock through 2007 and dominated the stock through 2011 when a smaller 2009/2010 cohort appeared (Demer and Zwolinski, 2012; Zwolinski and Demer, 2012).

After 1998, the PDO was increasingly negative. In particular, between 1999 and December 2012, 61% of the monthly PDO values were negative; and between January 2008 and December 2012, 85% were negative (in contrast, between 1981 and 1998, only 22% of the monthly PDO values were negative). Between 1999 and 2011, in concert with this relatively cold period, the assessment-derived reproductive success has been, on average, 30% of that observed in the previous 20 years. If we exclude from this analysis the three good recruitments between 2003 and 2005, observed during a short period with a positive PDO, the recruitment success was, on average, 14% of that observed during the sardine population expansion in the 1980s and the 1990s.

Although the behaviour of the PDO and that of multiple fish populations are often complicated by high frequency and unpredictable variability (Peterson and Schwing, 2003; Overland *et al*., 2008; Black *et al.,* 2011), the recent cold period in the northeast Pacific appears to be in agreement with the dominant ∼60-year component of the PDO, which is trending negative and its minimum is expected to occur between 2020 and 2025 (Figure 4; Zwolinski and Demer, 2012). If this signal continues to dominate in the future, and the environmental conditions that the PDO represents continue to predict sardine recruitment, the productivity of the stock will be low and yields will be reduced over the next decade. During extended periods of low recruitment, exploitation could exacerbate a decline in the stock (Jacobson and MacCall, 1995; PFMC, 1998) and both delay and stunt its recovery during the next period with favourable environmental conditions (Zwolinski and Demer, 2012). However, if an adequate seed biomass is maintained during the periods of average low productivity, unpredictable, short-term positive PDO episodes could intermittently yield surplus biomass.

Conclusion

We showed that the dynamics in oceanographic conditions described by fluctuations of the PDO explain the succession of sardine recruitment in the California Current during the last three decades. We showed that PDO-based indices for both the summer feeding season ($\mathrm{PDO}_{\mathrm{summer}}$) and the following spring-spawning season ($\mathrm{PDO}_{\mathrm{spring}}$) covary with sardine recruitment; and we provided an environmental Ricker model, parameterized with a “dual-phase” summer and spring PDO index ($\mathrm{PDO}_{\mathrm{combined}}$) and a condition factor to predict sardine recruitment. This implies that prespawning density-dependent energy storage is an additional mechanism for the compensatory effect implicit in the Ricker model fitted to sardine recruitment. All of these findings support our hypothesis that high recruitment occurs when oceanographic conditions are favourable for the parents during their summer feeding season, their condition factor is high, and the oceanographic conditions during the following spring-spawning season maximize early life stage survival. This data-supported hypothesis significantly augments the century-old theory that the reproductive success of coastal pelagic fish is governed by early life stage survival (Hjort, 1914; Lasker, 1978). Parental condition matters, too.

Acknowledgements

We thank Sean Hayes, Brian Wells, Nate Mantua, Bill Perrin, and Russ Vetter from SWFSC, and three anonymous reviewers and Jose Hidalgo for their constructive critiques and suggestions. We thank Kevin Hill and everyone involved in the assessment of the Pacific sardine. We also thank the persons responsible for producing and maintaining the environmental data time-series.

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Handling editor: Manuel Hidalgo

ICES Journal of Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2208–2220. doi:10.1093/icesjms/fst057

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Fisheries management under climate and environmental uncertainty: control rules and performance simulation

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Punt, A. E., A'mar, T., Bond, N. A., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., Haltuch, M. A., Hollowed, A. B., and Szuwalski, C. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. – ICES Journal of Marine Science, 71: 2208–2220.

Received 30 January 2013; accepted 26 March 2013; advance access publication 22 May 2013.

The ability of management strategies to achieve the fishery management goals are impacted by environmental variation and, therefore, also by global climate change. Management strategies can be modified to use environmental data using the "dynamic B_0" concept, and changing the set of years used to define biomass reference points. Two approaches have been developed to apply management strategy evaluation to evaluate the impact of environmental variation on the performance of management strategies. The "mechanistic approach" estimates the relationship between the environment and elements of the population dynamics of the fished species and makes predictions for population trends using the outputs from global climate models. In contrast, the "empirical approach" examines possible broad scenarios without explicitly identifying mechanisms. Many reviewed studies have found that modifying management strategies to include environmental factors does not improve the ability to achieve management goals much, if at all, and only if the manner in which these factors drive the system is well known. As such, until the skill of stock projection models improves, it seems more appropriate to consider the implications of plausible broad forecasts related to how biological parameters may change in the future as a way to assess the robustness of management strategies, rather than attempting specific predictions *per se*.

Keywords: climate change, global climate models, harvest control rules, management strategy evaluation, recruitment.

Introduction

The broad goal of fisheries management is to achieve a socially, economically, and politically acceptable trade-off among conflicting objectives. These objectives include achieving large and stable yields and profits and of conserving the fished resources and the ecosystems on which they depend to support future fisheries. A variety of scientific tools have been developed to assist in achieving this goal. These include stock assessment methods that generally estimate stock biomass and status relative to target, threshold and/or limit reference points, as well as harvest control rules (HCRs) that utilize the outcomes of the stock assessments to provide the scientific management advice on which decision-making is based.

In many jurisdictions, there is no direct link between the methods used to develop scientific management advice and the quality of the available data. However, several jurisdictions have now developed tier systems that link the choice of the HCR to

Table 1. Overview of the control rules used to provide overfishing limits (in principle, the catch which corresponds to the fishing mortality rate at which Maximum Sustainable Yield, F_{MSY}, is achieved) under the US Sustainable Fisheries Act [US Public Law 104–297] for fish stocks in the Gulf of Alaska and the Bering Sea (Reuter *et al.*, 2010).

	Data need for the tier control rule
Data-rich	
Tier 1	Reliable point estimates of B and B_{MSY} and reliable pdf of F_{MSY}
Tier 2	Reliable point estimates of B, B_{MSY}, F_{MSY}, $F_{35\%}$, and $F_{40\%}$
Tier 3	Reliable point estimates of B, $B_{40\%}$, $F_{35\%}$, and $F_{40\%}$
Tier 4	Reliable point estimates of B, $F_{35\%}$, and $F_{40\%}$
Data-poor	
Tier 5	Reliable point estimates of B and natural mortality rate
Tier 6	Reliable catch history from 1978–1995

be applied to the quality and the quantity of the data available (Table 1; Smith *et al.*, 2008). Management strategies are defined as combinations of data collection schemes, stock assessment methods, and HCRs selected to achieve prespecified management goals. Arguably, many of the systems used to provide scientific management advice can be considered to be management strategies. Some of these systems have been evaluated using simulation (i.e. using the management strategy evaluation, MSE, approach; Smith *et al.*, 1999; Punt, 2006; Butterworth, 2007; Rademeyer *et al.*, 2007, and those systems are frequently termed "management procedures") before their first application. However, the vast bulk of management strategies, particularly their HCR components, were developed by negotiation in committees rather than through simulation evaluation. Although such management strategies may appear sensible *a priori*, they need not be fully specified, and their likely performance in terms of achieving management goals remains unknown.

Management strategies have been developed and tested using simulation for a wide range of marine renewable resources, including (i) baleen whales subject to commercial and aboriginal whaling (e.g. Punt and Donovan, 2007), (ii) small pelagic fish, groundfish, and tunas (e.g. De Oliveira and Butterworth, 2004; Cox and Kronlund, 2008; Rademeyer *et al.*, 2008; de Moor *et al.*, 2011), and (iii) invertebrate stocks (e.g. Starr *et al.*, 1997; Johnston and Butterworth, 2005). Simulation has also been used to evaluate management strategies to achieve ecosystem objectives (e.g. Sainsbury *et al.*, 2000; Fulton *et al.*, 2007; Dichmont *et al.*, 2008). Most of these management strategies have been developed for data-rich commercially or recreationally important fisheries. However, increasingly, management strategies are being developed for data-poor and small-scale fisheries, for which traditional data sources such as fishery-independent survey data are either unavailable or unreliable (e.g. Dowling *et al.*, 2008; Smith *et al.*, 2009; Prince *et al.*, 2011).

Biological populations exhibit fluctuations due to the environment, and Hjort (1914) and many scientists subsequently identified plausible hypotheses relating environmental effects to changes in biological parameters. Several authors (e.g. Hofmann and Powell, 1998) have recommended that management strategies "must" include the effects of environmental variability. However, almost none do. An exception was the HCR used to provide management advice for Pacific sardine *Sardinops sagax* (Anon., 1998), for which the proxy for F_{MSY} was a function of temperature at Scripps Pier in La Jolla, USA. However, it has recently been shown (McClatchie *et al.*, 2010) that the relationship between log(recruits/spawner) and that measure of temperature is not significant ($p > 0.1$) when recent data on recruitment and spawner biomass were analysed. The method used to develop a proxy for F_{MSY} for Pacific sardine consequently had to be modified to remove the temperature-dependence of F_{MSY}.

Although the HCR for Pacific sardine was at least selected from among several HCRs following MSE-type simulation testing, Bay of Biscay anchovy, *Engraulis encrasicolus*, provides an example of the dangers of using environmental indices for management decisions without conducting such simulations first. Borja *et al.* (1998) found that an upwelling index was significantly correlated with the annual recruitment of Bay of Biscay anchovy for 1967–1996, explaining some 59% of the variability in recruitment. The corresponding relationship was subsequently used as a basis for predicting recruitment, which led to the estimate of spawning-stock biomass based on this prediction falling below an agreed precautionary threshold. The total allowable catch (TAC) for year 2000 was halved as a result (ICES, 2000, 2001). However, subsequent information indicated that the recruitment prediction was a substantial underestimate, leading ICES to conclude that the upwelling index had only limited use as a predictor of absolute recruitment (ICES, 2001, 2002). The practice of using the upwelling index to modify the TAC levels was subsequently abandoned. Part of the problem was that the environment–recruit relationship initially thought to be strong ($r^2 \sim 70\%$; Allain *et al.*, 2001) was subsequently shown to break down ($r^2 \sim 30\%$; Uriarte *et al.*, 2002). Subsequent simulation testing of this environmental index HCR concluded that precautionary approaches would better ensure successful management than using uncertain or moderate-to-weak environmental relationships (De Oliveira *et al.*, 2005).

The simulations used to evaluate the performance of candidate management strategies often consider a broad range of uncertainties related to the biological characteristics of the fished stocks such as variation in recruitment about the stock–recruitment relationship. However, simulations have tended to be based on the assumption that reality is identical with or very closely related to the assumptions on which stock assessments are typically based, e.g. by assuming time- and age-independent natural mortality, a stationary stock–recruitment relationship, and time-invariant somatic growth. However, the MSE approach can be used to explore violations of these assumptions, and, as shown below, violated assumptions are likely to be consequential and challenging for the development of management strategies that have the potential to achieve management goals under a wide variety of circumstances.

The examples above show that environmental and climate impacts on the population dynamics of marine species can be taken into account in the simulations used to evaluate management strategies and in the strategies themselves. These simulations can be used to evaluate the benefits of adopting a management strategy that explicitly accounts for environmental and climate impacts. This paper first outlines the way that management strategies are evaluated using simulation then provides a brief summary of the possible impacts of climate change and environmental variation on fish and invertebrate stocks and their associated ecosystems. Next, two basic approaches for evaluating the impact of climate change and environmental variation on the performance of management strategies are summarized. Finally, the key conclusions from a range of studies that have evaluated management strategies that do and do not explicitly allow for environmental change are reviewed, and directions for future work are suggested.

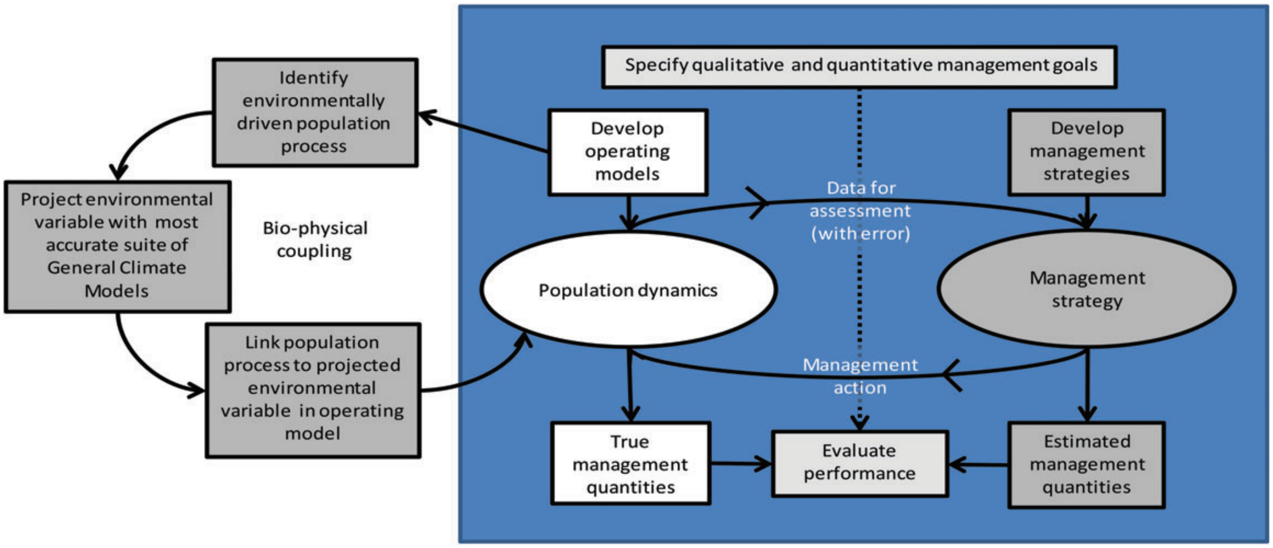

Figure 1. The MSE approach and how climate-induced factors can be used to drive the population dynamics of the operating model. The standard MSE framework is summarized in the box, and the links to environmental variables are indicated in the flowchart on the left side of the plot for the case in which the mechanistic approach is used. Note that the management strategy might make use of environmental data.

Evaluating management strategies using Monte Carlo simulation

MSE involves simulating the entire management cycle, including data collection, assessment, application of HCRs, implementation of regulations (which may not be perfect), and the consequences of removals on the population dynamics. The key steps when conducting MSE (Figure 1) are:

(i) identification of the management objectives and their representation using a set of quantitative performance measures;
(ii) development and parameterization of a set of alternative models of the system under consideration; each of these (operating) models provides an alternative plausible representation of reality, where the set is intended to capture the range of uncertainties that apply;
(iii) identification of alternative candidate management strategies that have the potential to achieve the management goals;
(iv) simulation of the future use of each candidate management strategy to manage the system as represented by each operating model under feedback control. Each simulation trial usually involves at least 100 replicates for a particular operating model. There are three steps for each time-step of the projection period:
  - generation of the types of data available for assessment purposes;
  - application of the management strategy to determine management actions; and
  - determination of the implications of these management actions by setting the removals from the "true" population for the next year based on these actions;
(v) summary of the simulation results by performance measures.

All these steps are important. However, given the focus of this paper, the key step is the selection of the uncertainties that will be captured in the operating models. The choice of uncertainties to include in an MSE depends on several factors, including the data available to parameterize the operating model and the time and computational resources available to conduct the analyses. Kell *et al.* (2006) identified two approaches for dealing with uncertainty related to model structure, i.e. model error.

(i) The operating model is the stock assessment model in current use. This provides a minimalist test—if the management strategy performs poorly when there is no model error, it is unlikely to perform well in the presence of model error.
(ii) The operating model is conditioned on existing data, but alternative operating models are considered, including those that postulate different drivers of the population dynamics into the future. The focus of this approach is on expert beliefs and other information about the processes that may affect the behaviour of management systems in the future. This is a less data- and more hypothesis-orientated approach. For example, studies of climate change may show that regime shifts that impact the average recruitment are possible, although such shifts have never been evident in historical datasets. Operating models that reflect this possibility could be developed to evaluate ways to provide management advice.

Possible impacts of climate change and environmental variation on management performance

Climate change and environmental variation can act as drivers of a wide array of biological processes that could be considered in MSEs. These include spatial distributions, migratory dynamics, spawning dynamics, fish availability to fishing and survey gear, and diet, as well as growth, survival, mortality, and recruitment rates.

Many species exhibit seasonal migrations between feeding and spawning grounds (e.g. Reid, 2001; Uriarte and Lucio, 2001; Agostini *et al.*, 2008; Sundby and Nakken, 2008) which could be subject to climate change and environmental variation. Change could impact migratory timing, extent, and behaviour (e.g. Huse and Ellingsen, 2008; Hare *et al.*, in press). For example, the timing of the commencement of the southwards prespawning migration of Northeast Atlantic mackerel, *Scomber scombrus*, has been linked to a change in water temperature (Reid, 2001), and there has been considerable variation in the timing and route of mackerel migration patterns between the 1970s and the 2000s (e.g. Walsh and Martin, 1986; Reid and Eltink, 1999). Mueter and Litzow (2008), Nye *et al.* (2009), and Last *et al.* (2011) document recent pole-ward shifts in the distributions of many other species, suggesting that migratory and distributional changes are already occurring. Changes in seasonal migrations and overall distributions will also impact the availability and vulnerability of fish to both survey and fishing gear, thus driving changes in selectivity and catchability. Such changes could impact the relationship between actual abundance and the indices of abundance on which stock assessments are based. An example of this is North Sea cod, *Gadus morhua*, for which one of the two multinational surveys has been dropped from the annual stock assessment because of a suspected change in survey catchability. This was caused by a change in migration behaviour due either to a northward shift in the stock within the survey area, resulting in changes in proportional availability to the vessels that make up the multinational survey, or to a change in local behaviour resulting in fish becoming less catchable by the survey (ICES, 2011).

Climate change is expected to impact the key vital rates of growth, survival, and natural mortality, either directly (e.g. due to physiological tolerances) or indirectly (e.g. due to predation or prey availability; e.g. Drinkwater *et al.*, 2010). Typically, the functional form of vital rate relationships is derived from combinations of retrospective studies, process studies, and laboratory experiments, but these relationships may not hold under climate change and environmental variation.

Recruitment to a survey or fishery is a function of survival across egg, larval, and juvenile life stages that is often described using a stock–recruitment relationship fitted to historical observations (Brooks and Powers, 2007). However, climate change would be expected to change both carrying capacity and the amount of recruitment at low stock size (Rose, 2004). Shifts in the climate regime have been shown to influence the recruitment of several species in the North Pacific. For example, Bering Sea Pacific cod *Gadus macrocephalus*, rock sole *Lepidopsetta bilineata*, flathead sole *Hippoglossoides elassodon*, and walleye pollock *Theragra chalcogramma* all experienced increases in recruitment after the 1977 regime shift (Conners *et al.*, 2002). The recruitment of Bristol Bay sockeye salmon *Oncorhynchus nerka* also increased after the 1977 shift (Adkison *et al.*, 1996). Hare and Mantua (2000) noted shifts in the recruitment of many species in 1977 and 1989. Control of the walleye pollock recruitment in the Gulf of Alaska appeared to shift from environmental effects on larvae to top-down predation on juveniles after the 1977 regime shift (Bailey, 2000). Similar regime shifts have been observed in the North Sea (Beaugrand, 2004) and the Baltic Sea (Alheit *et al.*, 2005).

Including climate change and environmental variation in operating models

The mechanistic approach

Several approaches are now available to integrate global climate models with models of biological populations (see review by Hollowed *et al.*, 2011, in press). The mechanistic approach to including climate change and environmental variation in an MSE involves integrating output from global climate models directly into the MSE framework (Figure 1). Kell *et al.* (2005) and Hollowed *et al.* (2009) summarize the basic approach, although it had been applied before their paper (e.g. Kell *et al.*, 2005). This approach involves (i) identifying mechanisms underlying the reproductive success, somatic growth, and distribution of the stock, (ii) assessing the feasibility of downscaling the implications of climate scenarios derived from global climate models developed by the Intergovernmental Panel on Climate Change (IPCC) for regional ecosystems to select and estimate relevant environmental variables, (iii) evaluating the extent to which environmental variables from IPCC models reliably predict changes in the values of the biological parameters of the stock, (iv) evaluating climate model scenarios and selecting IPCC models that appear to provide valid representations of forcing for the region of study, (v) extracting environmental variables from climate scenarios and incorporating them in projection models, and (vi) conducting projections where future management actions are determined by the candidate management strategies for each IPCC model.

A key step when applying this approach is to represent uncertainty appropriately. Apart from the estimation error associated with applying an assessment model to simulated data collected from the fishery, uncertainty is related to how well environmental variables are able to forecast the biological processes of interest (usually recruitment), as well as to the consequences of different IPCC forecasts. As will be outlined below, some studies have ignored these uncertainties, whereas others have attempted to represent them fully.

Future climate, and its variability, is being projected through model simulations that are being carried out internationally at more than 20 modelling centres. These models attempt to account for the complex and interacting atmospheric, oceanic, and terrestrial processes that determine the evolution of the global climate system. Stock *et al.* (2011) review current practices on the use of these models for marine ecosystem applications. Some issues identified in Stock *et al.* (2011) and related papers are discussed briefly below.

Two main sources of uncertainty feature in the climate simulations that form the basis for predictions of environmental factors. The first has been termed “structural” uncertainty. Whereas climate models are based on well-known and accepted physical principles, by necessity they can account for key processes in approximate ways only. Different choices have been made in the development of individual climate models, but the implications of these choices on the simulated climate are poorly understood. Hindcast simulations of past conditions are available from the models and have been compared with the observed climate and its variability (e.g. Overland and Wang, 2007), but past performance is not necessarily a good indicator of success in simulating future climate (Reifen and Toumi, 2009). This last conjecture is based on the evaluation of climate model errors, and in particular, the finding of little persistence in model skill from decade to decade in hindcast simulations validated against observations. This lack of persistence is perhaps attributable to the lack of stationarity in the processes responsible for climate variability. The models that are better at replicating some of these processes, such as ENSO, may be worse for others, such as sea ice impacts. The second main source of uncertainty is the inherent variability in the climate system. This system is chaotic, and the timing and phases of major and long-lasting fluctuations are largely unpredictable beyond time-horizons of a few years. Current climate models indicate that chaotic fluctuations will obscure the mean changes associated with long-term trends in many parts of the globe until the middle part of the 21st century (Wang *et al.*, 2010).

In principle, these two main sources of uncertainty can be addressed through the use of multimodel ensembles. An ensemble approach provides a means for accounting for both the natural, quasi-random swings in climate and the uncertainties in the models themselves by incorporating multiple simulations from a variety of models. Regarding model uncertainty, different models share common ancestries and attributes and are by no means independent. Moreover, structural uncertainties are pervasive to an unknown extent, and climate modelling includes assumptions about elements such as land use and greenhouse gas emissions that depend directly on future human activities. Nevertheless, an ensemble approach probably provides the best way currently available to develop a hopefully realistic range of potential outcomes of the climate related to the applications of interest.

The empirical approach

The mechanistic approach attempts to model changes formally over time in climate and the variables that might directly or indirectly drive the population dynamics of species under management. In contrast, the empirical approach allows for the impacts of climate change and environmental variation as well as ecosystem shifts by imposing trends in the values of some key parameters of the operating model that mimic plausible trends for those parameters, without attempting to link the operating model explicitly to, for example, IPCC models. An empirical approach is appropriate in cases where the impacts are postulated rather than supported by data, or where generic management strategies are being evaluated rather than management strategies that will be applied for a particular stock in a given ecosystem. This is because there are no actual environmental data available to use to relate to future changes in the parameters of the operating model. For example, Punt *et al.* (2012) examined the implications of changes over time in natural mortality, catchability, growth, and recruitment for the rock lobster *Jasus edwardsii* population off Victoria, Australia, on the performance of a proposed management strategy, although the evidence for climate change-induced effects on these parameters was weak to non-existent.

The evaluations of management strategies for commercial and aboriginal subsistence whaling by the International Whaling Commission (IWC) are perhaps the most thorough of such exercises. The evaluation of the IWC's "Catch Limit Algorithm" examined the implications of climate change and ecosystem shifts by imposing future trends in carrying capacity, natural mortality, and fecundity (IWC, 1992). Uncertainties related to trends in biological parameters were also considered during the evaluation of "Strike Limit Algorithms" used for the management of aboriginal subsistence whaling (IWC, 2003, 2005a).

Modelling of large-scale regime shifts provides an intermediate case between the largely mechanistic and purely empirical approaches. For example, A'mar *et al.* (2009a) and Szuwalski and Punt (in press) evaluated the impact of regime shift dynamics on recruitment by examining the existing time-series of recruitment estimates. They used these to specify scenarios related to the frequency with which regime shifts occur, the duration of a regime, and the extent to which expected recruitment changes during a regime shift. Sensitivity was explored by A'mar *et al.* (2009a) using a variety of scenarios regarding the length and frequency of recruitment regimes that were consistent with the available data.

The performance of management strategies that include or ignore climate-driven effects

Table 2 provides an overview of studies that have evaluated management strategies given climate-related trends in biological parameters but is restricted to those that captured the assessment error. Studies that involved projecting an operating model forward under constant fishing mortality are not included in Table 2 because it is not possible to control the fishing mortality rate directly. Rather, fishing mortality has to be adjusted using management measures such as catch limits, closed areas and times, and limits on vessel numbers or days-at-sea. There are, however, uncertainties in the relationships between such measures and their impact on fishing mortality, and ignoring those uncertainties may lead to severe underestimation of the true extent of uncertainty associated with the ability to manage the system.

The focus of Table 2 and this section is on modelling climate effects on biological parameters, and whether robust management strategies can be identified. The most common ways to (attempt to) use environmental data in management strategies are as follows:

(i) The "dynamic B_0" approach (MacCall *et al.*, 1985). This involves setting the unfished unexploited biomass, B_0, used when applying HCRs to the average spawning-stock biomass calculated projecting the population forward from the first year with catches until the current year, without fishing. The values for all of the parameters of the model, including the deviations in recruitment about the stock–recruitment relationship, are set at the values estimated in the stock assessment when making this projection. The "unfished" biomass will vary over time because of the estimated recruitment deviations as well as any time-varying aspects of growth and natural mortality.

(ii) The "moving window" approach (Figure 2). This involves basing biomass reference points such as B_0 and B_{MSY} on the estimates of recruitment for the last x years, often 20–25 years to ensure that there are sufficient datapoints for the biomass reference points to be estimated with reasonable precision. This method implies that the estimates of B_0 and B_{MSY} change over time, hopefully allowing them to reflect the "current environmental conditions".

(iii) The STARS approach (Figure 2). This is similar to the moving window approach, but uses the STARS algorithm (Rodionov, 2004; Rodionov and Overland, 2005) to select the set of recent years on which reference points are based. STARS assumes a minimum duration of a regime and defines a "previous regime" based on that assumed minimum regime duration and available data. Next, the deviations of each new year's datum from the previous regime's average are compared with a t-distribution defined by the mean and standard deviation of the mean of the observed data for the previous regime. A new regime is considered to have possibly begun when the deviation for the new year is significantly different (e.g. $p < 0.1$) from the mean for the previous regime. The differences in each

Table 2. Summary of studies that have evaluated the robustness of the management systems to climate-induced trends in biological parameters.

Species	Biological parameters impacted	How modelled	Management strategies	Reference
Mechanistic				
Gadus morhua	Recruitment, growth	Linked to temperature. (i) no change in temperature; (ii) linked to the HadCM3B1 model; (iii) a constant rate of increase in temperature	An extended survivors analysis linked to a HCR which allowed for a predicted increase in biomass	Kell *et al.* (2005)
Theragra chalcogramma	Recruitment	Linked to predicted climate variables from eight IPCC models	NPFMC Tier 3 HCR with B_{MSY} based on (i) all recruits and (ii) a "dynamic" B_{MSY} approach	A'mar *et al.* (2009b)
Sardinops melanostictus	Recruitment	Linked to SST in the nursery area	Constant fishing mortality; a threshold management strategy; a variant of the threshold management strategy in which catches are reduced when temperature drops exceeded a cut-off	Hurtardo-Ferro *et al.* (2010)
Sebastes alutus	Recruitment	Linked to the date of spring transition. Scenarios related to the time-trend in the delay in spring transition	Management strategies based on an age-structured stock assessment model linked to a control rule which includes a formal rebuilding analysis. Sensitivity to knowing the change in the date of spring transition	Punt (2011)
Theragra chalcogramma	Recruitment	Linked to predicted climate variables from 82 IPCC models	NPFMC Tier 2 HCR with (i) fishing mortality dropping before the stock drops below B_{MSY}; (ii) B_0 based on a 20-year moving window; (iii) B_0 dependent on recent recruitment and contribution to spawning biomass; and (iv) different caps on the catch of pollock	Ianelli *et al.* (2011)
Chionoecetes opilio	Recruitment	Linked to predicted climate variables from 10 IPCC models	NPFMC Tier 3 HCR with B_{MSY} based on (i) all recruits and (ii) recruits based on the STARS algorithm	Szuwalski and Punt (in press)
Eschrichtius robustus	Birth and survival rates related to sea ice in the Bering Sea	Related to ensemble mean forecast of sea ice in the Bering Sea (March–April average)	The IWC Gray Whale *Strike Limit Algorithm*	Brandon and Punt (in press)
Empirical				
Sardinops sagax	Recruitment	Autocorrelated about a Ricker stock–recruitment relationship with a 60-year cycle	Threshold strategy with parameters for F_{MSY} and the cut-off at which F is zero	Anon. (1998)
Generic Baleen whale	Carrying capacity; natural mortality; productivity	Linear increases and decreases; cycles	The IWC *Catch Limit Algorithm*	IWC (1992)
Balaena mysticetus	Carrying capacity; natural mortality	Linear increases and decreases; cycles	The IWC Bowhead Whale *Strike Limit Algorithm*	IWC (2003)
Eschrichtius robustus	Carrying capacity; natural mortality	Linear increases and decreases; cycles	The IWC Gray Whale *Strike Limit Algorithm*	IWC (2005a)
Sardinops sagax; *Engraulis encrasicolus*	Carrying capacity	Cyclic	The joint Anchovy-Sardine HCR (De Oliveira and Butterworth, 2004): (i) unchanged and (ii) modified to account for knowledge of changes in productivity	De Oliveira (2006)
Merluccius capensis and *M. paradoxus*	Carrying capacity	Decrease linearly by 30% from 2007 to 2011; constant thereafter	Empirical management procedure	Rademeyer *et al.* (2008)
Theragra chalcogramma	Recruitment	Step function changes	NPFMC Tier 3 HCR with B_{MSY} based on (i) all recruits; (ii) recruits selected using the STARS algorithm; (iii) a moving average of recruits; and (iv) a 'dynamic' B_{MSY} approach	A'mar *et al.* (2009a)
Antarctic krill	Biomass	Constant rate with time	Management by small management areas	Plagányi *et al.* (2011)
Jasus edwardsii	Recruitment, growth, catchability, natural mortality	Linear trends with time	Strategy inferred from the intent of the government of Victoria	Punt *et al.* (2012)
Bêche-de-mer	Natural mortality and growth	Step function reductions	Twelve strategies, including spatial strategies	Plagányi *et al.* (2011)

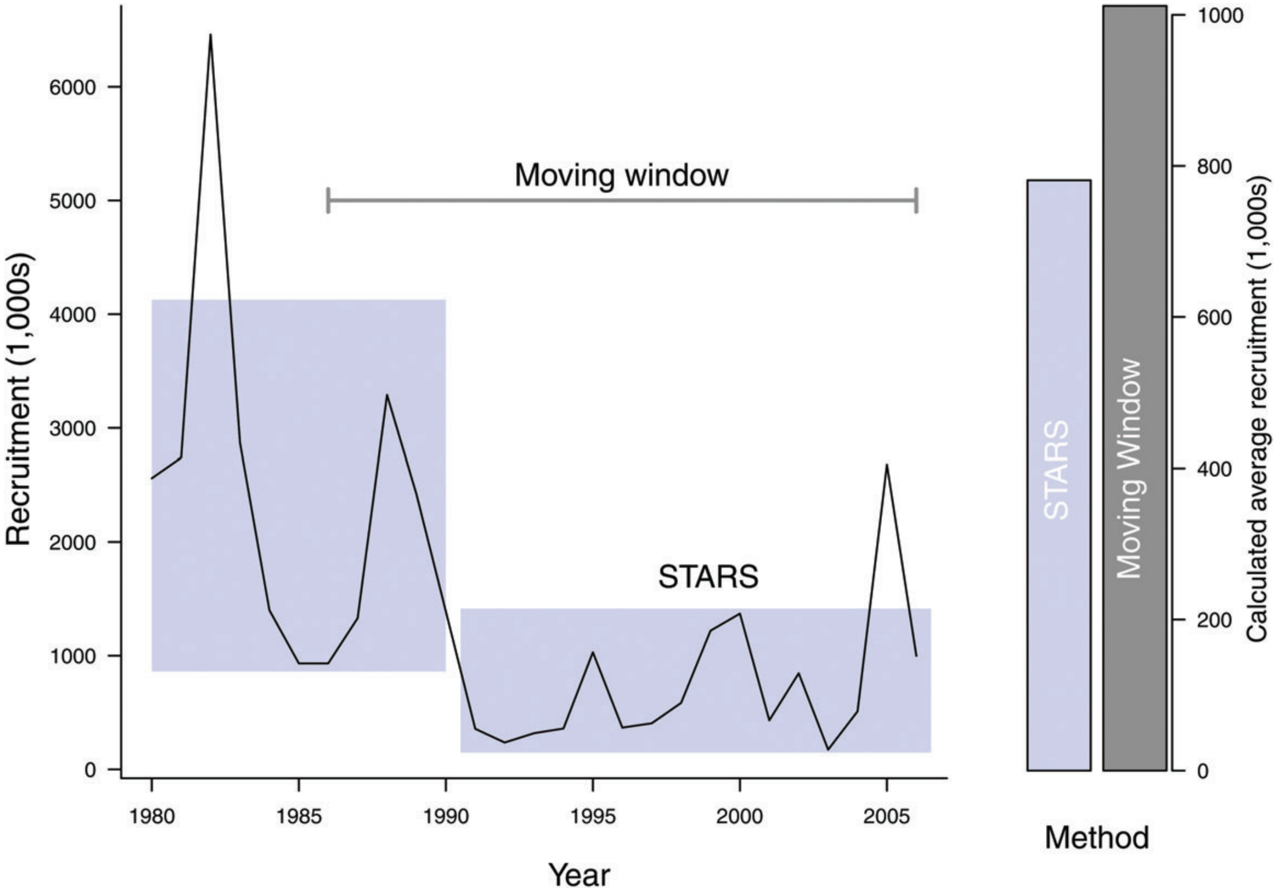

Figure 2. Application of the moving window and STARS approaches for calculating the mean recruitment. The moving window approach in this example always sets the mean recruitment using the most recent 20 years of recruitment estimates, whereas the STARS approach would set the mean recruitment to the mean of the most recent shaded set of recruitments or a new block of recruitments if a new recruitment regime is detected. Note that the recruitments and the average recruitments are on different scales.

subsequent year's deviation from the previous regime average are tallied after the first significant excursion from the previous regime average. A shift in regime is confirmed when the algorithm has progressed a number of years into the "new" regime equal to the minimum assumed duration of the regime, provided the running tally does not change sign (i.e. if the original excursion from the mean was positive, then if the running tally becomes negative, the initial year is no longer considered as the potential start of a new regime and the algorithm moves on). The set of years used to define the mean recruitment when applying the HCR are those for the most recent recruitment regime.

Analyses based on the mechanistic approach

Kell *et al.* (2005) evaluated management strategies for Atlantic cod in the North Sea in which both growth and recruitment were linked to temperature forecasts from an IPCC model. Climate change had little impact on the short-term results, but greater impact over the longer term. Incorporating environmental covariates into the existing management strategies did not lead to markedly better outcomes. Kell *et al.* (2005) highlighted the fact that HCRs that use biological reference points based on fishing mortality appear to perform more robustly than those based on biomass reference points when the somatic growth and recruitment dynamics are driven by climate.

A'mar *et al.* (2009b) considered two management strategies for Gulf of Alaska walleye pollock. The analysis explicitly recognized the uncertainty associated with: (i) linking the environmental covariates considered (precipitation and SST) with recruitment, (ii) the values of the parameters that govern the relationships between the covariates and recruitment, and (iii) the predictions of precipitation and SST from eight IPCC models. The results were highly dependent on the choice of the IPCC model, underscoring the importance of considering a range of plausible IPCC models when applying the mechanistic approach. The performance of a "dynamic B_0" management strategy was not markedly better than a management strategy that ignored links between climate and recruitment.

Hurtardo-Ferro *et al.* (2010) used the relationship between SST and deviations in recruitment about a Ricker stock–recruitment relationship for Japanese sardine *Sardinops melanostictus* as the basis for an evaluation of management strategies. Future SST values were generated by randomly selecting whether a change in the SST regime occurred, then sampling an SST value given the regime. The management strategies evaluated were constant fishing mortality, a threshold strategy that reduced fishing mortality when biomass dropped below a specified level, and a variant of the second strategy in which fishing mortality was reduced if SST exceeded a threshold value. The last two strategies outperformed the constant fishing mortality rate, with the strategy based on SST marginally outperforming the standard threshold strategy.

Punt (2011) evaluated the performance of a management strategy that mimics how management advice is provided for Pacific ocean perch *Sebastes alutus*, a rockfish off the US west coast that is currently under a rebuilding plan and for which recruitment is related to the date of spring transition. This study found that knowing how spring transition will change in future did not improve the performance of the management strategy appreciably.

Ianelli *et al.* (2011) analysed the performance of management strategies for walleye pollock in the eastern Bering Sea. In contrast to several other studies, they concluded that the management strategy currently used to provide management advice, which does not change reference points as a function of ecosystem state, will result in much smaller average catches and an increased likelihood of fishery closures should warming continue and that other HCRs could perform markedly better.

Analyses based on the empirical approach

A'mar *et al.* (2009a) calculated the impact of regime-shift changes in the mean recruitment on walleye pollock in the Gulf of Alaska. Ignoring regime shifts when providing management advice led to higher biomasses and lower rates of fishing mortality. In contrast, basing the average recruitment used to define management reference points on a 25-year sliding window achieved higher catches, but at the cost of a higher risk of fishing mortality exceeding the overfishing limit.

Punt *et al.* (2012) evaluated the performance of the management strategy that can be inferred from the management plan for rock lobster off Victoria, Australia. Changes over time in natural mortality and growth were relatively inconsequential for the performance of the strategy, and estimating time-varying growth from tagging studies allows for such changes to be taken into account in assessments. In contrast, trends in catchability and recruitment led to a failure to achieve management goals.

Rademeyer *et al.* (2008) considered the impact of assumed changes to past and future carrying capacity on a management strategy for the South African hake resource, which consists of two species, *Merluccius capensis* and *M. paradoxus*. The below-average estimated recruitment during the 1990s and early 2000s for *M. capensis* suggested a possible systematic deviation from the assumed stock–recruitment relationship, prompting consideration of a scenario in which carrying capacity for this species dropped in 1992. An alternative scenario assumed a reduction in carrying capacity for both hake species in future years. The performance statistics were robust to these scenarios, except that a decrease in the simulated future catches was predicted when a lower future carrying capacity was assumed.

Plagányi *et al.* (2011) developed a multispecies spatial operating model to evaluate the impacts of climate change on catches and abundance of sea cucumber in the Torres Strait region of northern Australia. A reference set of factors was developed for the MSE. Different species reacted differently to climate change. Strategies based on spatial management performed well in data-limited situations, whereas those that controlled fishing mortality did well in data-rich situations.

De Oliveira and Butterworth (2005) investigated how the expected yield is related to the proportion of variation in recruitment explained by an environmental index. They found that environmental indices need to explain at least 50% of the total variation in recruitment (coefficient of determination, $r^2 > 0.5$) before management strategies showed any benefits in terms of risk and average catch. For lower r^2, performance was worse in terms of the average catch when incorporating the environmental index compared with ignoring it.

Walters (1989) investigated expected improvements in management performance resulting from the use of recruitment forecasts. He found that these depended strongly on the average productivity of the stock concerned, and the flexibility of the in-season regulatory system used to manage that stock. For example, productive stocks managed with inflexible annual catch limits showed large improvements in the average yield if perfect preseason forecasting was practical, but unproductive stocks showed only modest improvements regardless of the in-season regulatory system used.

Discussion

Despite 100 years having passed since Hjort's (1914) work, there is still considerable uncertainty about the functional relationship between spawners and recruits and how environmental variability influences this relationship, along with other biological processes. That said, it is now possible to model complex non-linear relationships through time and space, although not within the context of actual stock assessments. Operating models within an MSE can, however, be used to explore factors that cannot be included in standard stock assessment methods, to determine if (i) management is robust to the omission of the complex effects that cannot be modelled and predicted definitively, (ii) it is possible to identify new management systems that are robust to these effects, or (iii) the key areas of monitoring and process research needed to resolve the processes can be identified.

Including environmental and climate drivers in the operating models used to evaluate management strategies

Relatively few papers have evaluated management strategies given climate-induced changes in biological parameters. In contrast, many studies have identified putative relationships between biological parameters, usually recruitment, and environmental covariates (e.g. Chen, 2001; Cook and Heath, 2005; Sinclair and Crawford, 2005; Arregui *et al.*, 2006). This suggests that the mechanistic approach could be applied for the associated stocks. For example, Wilderbuer *et al.* (in press) predicted that the recruitment of three Eastern Bering Sea flatfish stocks: flathead sole (*H. elassodon*), northern rock sole (*Lepidopsetta polyxystra*), and arrowtooth flounder (*Atheresthes stomias*) may occur under future climate scenarios.

The option of basing forecasts on models that link biological parameters to environmental variables is attractive in principle and seems to be more biologically realistic than the empirical approach. However, while providing useful information retrospectively, understanding the mechanisms underlying shifts in production is necessary to project future responses to climate variability and change. Furthermore, care should be taken when interpreting the results of such forecasts given (i) the possibility that relationships might be false (Haltuch and Punt, 2011), (ii) the likelihood that once-significant relationships may break down in time as additional monitoring data become available (Myers, 1998; McClatchie *et al.*, 2010), (iii) the poor ability to make predictions of environmental variables beyond a few years into the future (e.g. Walters and Collie, 1988), and (iv) the likelihood that the form of the relationship will change over time (Schindler *et al.*, 2008). Furthermore, results of the forecasts may be highly sensitive to the models used to forecast the environmental variables (e.g. A'mar *et al.*, 2009b).

The outcomes from the empirical approach naturally cannot be treated as predictions because the drivers of the biological parameters of the operating model are not based on the actual estimated relationships. As such, the main value of this approach is to explore the extent to which management strategies are likely to be robust to changing biological parameters.

Within the United States, key criteria used to measure the success of fishery management are maintaining stock size above a minimum stock size threshold (MSST) and restricting fishing mortality to beneath the maximum fishing mortality threshold (MFMT). Both the MSST and the MFMT are well-defined for single-species fisheries in which biological parameters are time-invariant. Defining the MSST and the MFMT when calculating the performance statistics used to quantify the behaviour of management strategies is a key challenge associated with allowing biological parameters to change over time in an MSE. Several proposals have been developed to address this. For example, the IWC has expressed the results from forecasts as the population size relative to that which would have eventuated had no exploitation taken place, in an attempt to "scale out" the effects of time-varying biological parameters. In contrast, other studies (e.g. A'mar *et al.*, 2009a, b; Szuwalski and Punt, in press) have calculated quantities such as the MSST for the current regime. However, none of these solutions is ideal, and concern remains about how to interpret the results of simulations in which the values for biological parameters change over time.

The use of the STARS algorithm to define the current regime can lead to marked changes in perceived stock status. For example, changing the years used to define the MSST could lead to a stock that was previously "healthy" being defined as overfished (or *vice versa*).

Management strategies sometimes contain exceptional circumstances provisions that lead to an automatic review of the management strategy and perhaps additional restrictions on the fishery if resource monitoring data fall outside of the expected range (e.g. Rademeyer *et al.*, 2008; de Moor *et al.*, 2011). In principle, these provisions could make an overall management strategy robust even in the face of time-trends in biological parameters. However, whether this approach will perform satisfactorily has not been evaluated yet and may prove difficult using simulation because it would require that the measures applied when exceptional circumstances arise be specified, which is not currently the case.

It is self-evident that the performance of any management strategy will be poor under some scenarios regarding, for example, the impact of climate change. Furthermore, it is also likely that the relative performances of management strategies will depend on how much weight is placed on the hypotheses underlying simulation trials with such time-trends. Therefore, it is necessary to consider the relative plausibility of different scenarios. Butterworth *et al.* (1996) proposed the following four-level scheme to assign plausibility ranks to the hypotheses underlying alternative operating models:

(i) how strong is the basis for the hypothesis in the data for the species or region under consideration;
(ii) how strong is the basis for the hypothesis in the data for a similar species or another region;
(iii) how strong is the basis for the hypothesis for any species; and
(iv) how strong or appropriate is the theoretical basis for the hypothesis?

This scheme was presented to the Scientific Committee of the IWC in 1995, but it was 10 more years before circumstances had developed to the stage that the Committee needed to agree on some approach. At that time, a less formal approach, involving a Delphi method, in which the Committee assigns a plausibility ranking of high, medium, low, or no agreement to alternative operating models was agreed and applied (IWC, 2005b). Operating models assigned a plausibility of low are ignored, and the acceptable risk for operating models that are assigned medium plausibility is higher than for operating models assigned high plausibility.

The issue of plausibility is more challenging for the empirical approach to modelling the impacts of climate on biological parameters. This is because although mechanistic models may break down given additional data, they are usually motivated by sound ecological principles and the strength of any relationships between environmental variables and biological parameters is based on actual data. In contrast, the strength of an empirical relationship tends to be an educated guess (e.g. Punt *et al.*, 2012), which makes determining plausibility much more difficult. This would not matter if the management strategy being applied showed robust performance independent of that strength. However, feedback control is not perfect and hence often unable to effect sufficient self-correction to continue to achieve management goals under more extreme scenarios. Furthermore, even in cases where it does work well, there may be discomfort at accepting the reduced biomass target reference point which this may imply. Therefore, even under the empirical approach, there remains a need for research to attempt to improve these educated guesses of the strengths of the environment's impact on biological processes.

The operating models considered in past studies have generally been based on single-species population dynamics models. However, it is possible to base evaluations of management strategies on more complicated operating models that represent the links between climate and biological responses for targeted species more explicitly. For example, the *Atlantis* model (Fulton *et al.*, 2007, 2012) is a fully spatially resolved ecosystem model that can be forced using climate model predictions. Although *Atlantis* has yet to be used to evaluate management strategies given climate impacts, this is clearly a future research direction. This is particularly the case if one of the future effects of climate change will be changes to species distributions and hence predator–prey relationships. Dynamic ocean features include changes in temperature, salinity, current strength, hypoxic zones, the oxygen minimum zone, and the mixed layer depth that influence the distribution, abundance, or growth of marine fish. These could be used to now-cast using real-time environmental conditions (e.g. Howell *et al.*, 2008; Lehodey *et al.*, in press) or forecast changes in stock migrations and distribution (Fogarty *et al.*, 2008).

Should management strategies be designed respond to climate and environmental variation?

Several ways to modify the existing management strategies for better performance in face of climate- and environmentally induced drivers have been suggested. These include the dynamic

B_0 approach, computing reference points using a moving window of model outputs (e.g. A'mar *et al.*, 2009a) and applying the STARS approach (e.g. A'mar *et al.*, 2009b; Szuwalski and Punt, in press). However, all these approaches base reference points and hence HCRs on a subset of the estimates of biomass and recruitment, or estimate additional parameters. This can lead to greater variance that explains, for example, the result of Szuwalski and Punt (in press) whereby management strategies that attempt to account for changes in productivity over time can actually lead to greater risk when there are no such changes.

Many of the studies covered in detail above, along with more generic studies, such as those of Basson (1999), De Oliveira and Butterworth (2005), De Oliveira (2006), and Brunel *et al.* (2010), found that modifying management strategies to include environmental covariates did not improve the ability to achieve management goals over time-scales relevant to short- and medium-term fisheries management decision-making much, if at all. They did so only if information on the environmental factors driving the system were very well known. Whether this conclusion holds over the very long-term has yet to be fully evaluated, although many climate impacts and differences among ensemble projections only become substantial many decades into the future.

The inability, usually, of management strategies that include environmental covariates to outperform those which do not contrasts with the conclusion of King and McFarlane (2006). They found that accounting for the knowledge of changes in the regime could lead to improved management performance (although they did not model assessment error and assumed instead that fishing mortality rates could be implemented directly). The results from the reviewed studies are therefore more consistent with the conclusions of Walters and Parma (1996) that harvesting a constant proportion of the stock each year in the face of climate change leads to long-term yields that are likely to be within 15% of optimum possible yields. As such, and as suggested by Szuwalski and Punt (in press), until the skill of stock projection models improves, it seems more appropriate to consider the implications of plausible broad forecasts related to how biological parameters may change in the future as a way to assess robustness of management strategies, rather than as specific predictions *per se*.

Acknowledgements

Tony Smith and Éva Plagányi (CSIRO Marine and Atmospheric Research), Andy Payne (CEFAS), Owen Hamel (NWFSC, NOAA), and three anonymous reviewers are thanked for their comments draft of this paper. AEP acknowledges support from NOAA Grant NA10OAR4320148. This is BEST-BSIERP Bering Sea Project publication #102, NPRB publication #425, PMEL contribution #4006, and JISAO contribution #2119.

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Handling editor: Howard Browman

ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2221–2230. doi:10.1093/icesjms/fst150

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Predator–prey population models of migrant insects with phase change

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Cheke, R. A., Tang, S., and Tratalos, J. A. Predator–prey population models of migrant insects with phase change. – ICES Journal of Marine Science, 71: 2221–2230.

Received 10 June 2013; accepted 13 August 2013; advance access publication 16 September 2013.

Locusts and some noctuid moths exhibit polyphenism whereby they can change their "*phase*" from a solitary ("solitarious") condition to a gregarious one. Gregarious *phase* insects are often migratory travelling from recession areas into larger invasion zones and, among locusts, occur in swarms. Difference equation models of the population dynamics of insects that take account of such changes between solitarious or gregarious *phases* in relation to predation, both with and without time delays, are described. Solutions of the models are non-linear. Chaotic solutions are obtainable under some circumstances even with very low values for the intrinsic rate of increase in the prey population, in contrast to previous conclusions from models without predation. Comparisons with the results obtained for single species with those obtained in this paper show that predation can reduce (i) the average density of the prey, (ii) durations of periods when the populations stay in the gregarious *phase*, and (iii) the frequency of their shifts from the solitarious state to the gregarious form. Similar results are obtained if a time delay is introduced to mimic a transient *phase*. With a wide range of parameter values, models including predation with or without random perturbation reveal several stable attractors for phase diagrams of the populations, which are biologically meaningful compared with empirical datasets and which were unobtainable without predation, suggesting that inclusion of predation and time delays improved the realism of the models. However, comparisons between autocorrelation analyses of locust time-series, but of swarms only, with those of model outputs suggest that inclusion of the time delay leads to less, not more, realism. The prediction of non-linearity in the dynamics of migrant insects with *phase* changes and its significance for forecasting to aid control is briefly discussed in relation to published data on the desert locust *Schistocerca gregaria*.

Keywords: armyworm, attractor, bifurcation, Holling's disc equation, locust, polyphenism, predation, *Schistocerca gregaria*, *Spodoptera exempta*, time-lags.

Introduction

In his seminal paper on fish population dynamics, the centenary of which is celebrated in this special issue, Hjort (1914) sought reasons why fish catches in Norwegian waters and elsewhere were extremely variable. One cause of the fluctuations was the irregular nature of the amount of recruitment to the populations and the influence of this irregularity on subsequent fish stocks and hence yields. Crucially, Hjort identified how age structure was part and parcel of how populations could be followed and data on age distributions used to make predictions about future dynamics. Such insight led to modern modelling methods for determining harvest quotas that allow maximum sustainable yields (Beverton and Holt, 1956), if the timing of catches are taken into account for optimal harvesting strategies (Tang *et al.*, 2006). In such models, fish are not treated as being morphologically or behaviourally plastic, but it is now known that some species exhibit polyphenism. This includes variation in behavioural traits such as foraging depth and migration activity of Atlantic Cod *Gadus morhua* that may influence their catchability and evolution under predation pressure (Jørgensen *et al.*, 2008; Fiksen and Jørgensen, 2011). At least six families of freshwater fish are polyphenic (Robinson and Parsons, 2002) and some species show behavioural polyphenism with different individuals being "bold" or "shy" (Sneddon, 2003), in addition to the extraordinary phenomenon found in fish, such as the economically important salmon *Salmo* spp. and other anadromous species, that migrate between freshwater and marine environments. Extreme variability, age structures, polyphenism, geographical range changes, and human interventions also characterize the dynamics of locusts. It is the ability of locusts to change their physiology, morphology, behaviour, and migratory habits which stands them apart from most other insects. Another theme common to fish, as addressed by Hjort, and to locusts is the need to analyse long time-series in searches for explanations of their population dynamics. However, an important difference is that it is generally sought to minimize locust populations but maximize the yield from fish.

In addition to locusts, among insects, there are species of moth that exhibit polyphenism and can change their "*phase*" (italicized throughout this paper to distinguish this character from the use of phase in the term "phase diagram", see below) from a solitary condition to a gregarious form. The latter is usually associated with a migratory habit and may involve cohesive flight behaviour such as swarming, as is true with locusts such as the desert locust *Schistocerca gregaria*, migratory locust *Locusta migratoria*, and the red locust *Nomadris semptemfasciata*. When locusts are at low densities and in the solitarious condition, they are referred to as being in *recession*, in contrast to high density, *plague*, populations that form swarms and migrate long distances. Many of the species exhibiting *phase* changes are pests and, as such, have received much attention from biologists but there have been few attempts to take account of *phase* in models of their populations. Changes from a "solitarious" *phase* to a gregarious one by locusts involve alterations in their behaviour, morphology, and physiology (Uvarov, 1921, 1966, 1977; Pener, 1991; Tanaka, 2006; Pener and Simpson, 2009), resulting in changes in intrinsic rates of increase (Cheke, 1978) and carrying capacities which have implications for their population dynamics (Holt and Cheke, 1996; Ibrahim, 2001). Some other groups also exhibit *phase* polyphenism, examples being certain species of noctuid moths (Brown, 1962; Iwao, 1962, 1967), with similar effects on rates of reproduction (Cheke, 1995). For instance, caterpillars of solitarious forms of the African armyworm moth *Spodoptera exempta* are green, but gregarious caterpillars are black and move together in "armies" (Faure, 1943; Matthée, 1946). Although their adults do not form coherent swarms, the gregarious *phase* of *S. exempta* is also migratory: moths emerge synchronously, from fields where marching groups of its larvae have pupated, then take flight together (Riley *et al.*, 1983; Pedgley *et al.*, 1989). There is, however, evidence that increased migratory activity may be involved in a trade-off with reproductive success (Gunn *et al.*, 1989).

The population dynamics of such species with *phase* change are not fully understood, although it is known that a variety of mechanisms associated with increases in population densities and environmental influences can trigger the changes in *phase* (Uvarov, 1966, 1977; Simpson *et al.*, 1999). Among the locusts, there are usually clearly defined outbreak areas where populations increase to levels sufficiently high for gregarization to occur, leading to migrations and invasions by swarming populations into larger "invasion" areas outside the outbreak zone or zones (Uvarov, 1977; Steedman, 1990). Unlike most other locust species, the desert locust does not have one or two discrete outbreak areas but many gregarization zones within a "recession" area of ~16 000 000 km^2, which is approximately half the size of the huge invasion area of 29 000 000 km^2 (Uvarov, 1977; Centre for Overseas Pest Research, 1982) that extends into more than 60 countries and covers >20% of the total land surface of the earth (Hemming, 1968), into which swarms may spread. For this reason, the carrying capacity of gregarious locusts is taken as being greater than that of solitarious forms in the models described below. Although less well defined, *S. exempta* also has zones (e.g. the Morogoro area of Tanzania) from where the first outbreaks of a season tend to occur (Rose *et al.*, 1995). Preventive control strategies against both locusts (Steedman, 1990; Sword *et al.*, 2010) and armyworm (Cheke and Tucker, 1995; Rose *et al.*, 2000) emphasize the need to control population densities within outbreak zones.

Here we re-describe a model of insects with *phase* change, previously presented by Holt and Cheke (1996), which can be used to simulate and predict the insects' population dynamics for comparisons with observed data, but the novelty of this paper is that we extend the model to include, first, predation and then a time delay as well. Numerical analyses of the models show dynamical behaviour which is very complex, including stable equilibria, multi-point cycles, and chaos. Partly because empirical estimates of the intrinsic rate of increase (r) for gregarious desert locusts have often been above 4 and ranged up to 10.78 per generation (Cheke, 1978; Blackith and Albrecht, 1979; Farrow and Longstaff, 1986), it was suggested by Cheke and Holt (1993, 1996) and Holt and Cheke (1996) that locusts might have chaotic dynamics. However, these authors assumed that this would only be possible if the value of the intrinsic rate of increase for gregarious insects was above the threshold (2.692) for chaos in the logistic map (May, 1974, 1976), which we show here is not necessarily the case.

By expanding the model of Holt and Cheke (1996) with the inclusion of predation and time-lags, we show that not only are non-linear dynamics predicted but that, under some circumstances, chaotic outcomes are possible with relatively low values of the intrinsic rate of increase. Furthermore, the new models presented here show that predation can significantly reduce the average density of the prey population, reduce periods when locust populations are gregarious, and reduce the frequency of locust population shifts from the solitarious state to the gregarious form. Similar but more complicated results are obtained after introduction of a time delay, mimicking the intermediate transient *phase*. Furthermore, multi-point cycle solutions are possible, with or without the time delay, predicting *phase* changes from a low-density solitary condition via an intermediate transient *phase* to a high-density gregarious form and back again. Also, some of the various attractors of the models, including multi-point cycle and chaotic attractors, resemble phase diagrams of actual locust dynamics based on field data of numbers of geographical units infested (Figures 1–3).

Models

Logistic population models with switches in *r* and *K*

The models were derived from the well-known logistic population growth model [Equation (1)] and the locust phase change model of Holt and Cheke [1996; Equation (2)] as described below:

$$x_{t+1} = x_t \exp\left(r\left(1 - \frac{x_t}{K}\right)\right) \qquad (1)$$

where x_t is the population density at time t; r the intrinsic rate of increase; K the carrying capacity of the environment.

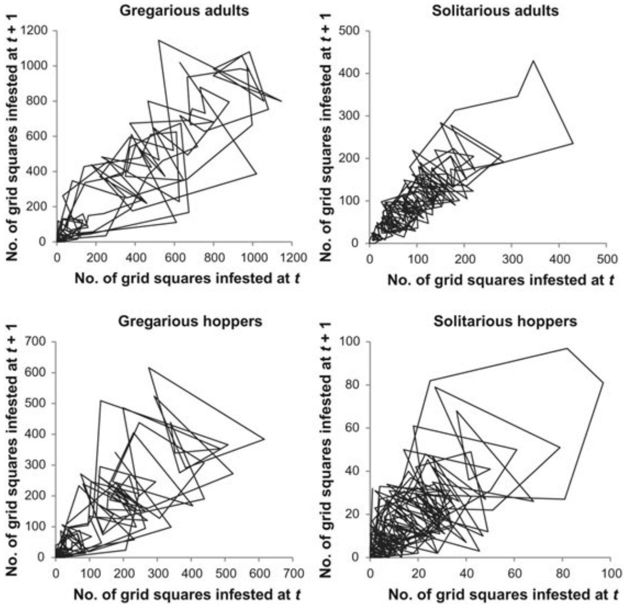

Figure 1. Phase diagrams (numbers at time t, plotted against numbers at $t + 1$, those at $t + 1$ plotted against numbers at $t + 2$ etc.) of 4-monthly data for the number of 1° grid squares reported as infested with desert locusts *S. gregaria* for the years 1930–1999 inclusive for gregarious adults (swarms), solitarious adults, gregarious hoppers, and solitarious hoppers (FAO SWARMS dataset).

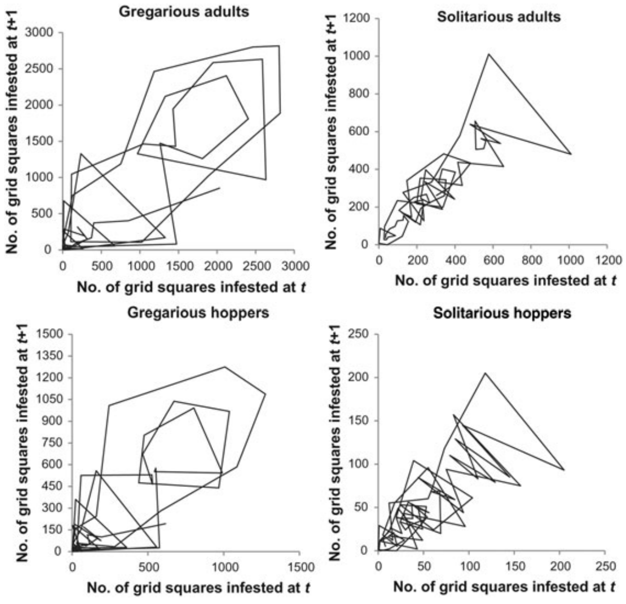

Figure 2. Phase diagrams (see Figure 1 for explanation), numbers in year N plotted against numbers in year $N + 1$, of the data in Figure 1 summed to become annual data for desert locusts *S. gregaria* for the years 1930–1999 inclusive for gregarious adults (swarms), solitarious adults, gregarious hoppers, and solitarious hoppers (FAO SWARMS dataset).

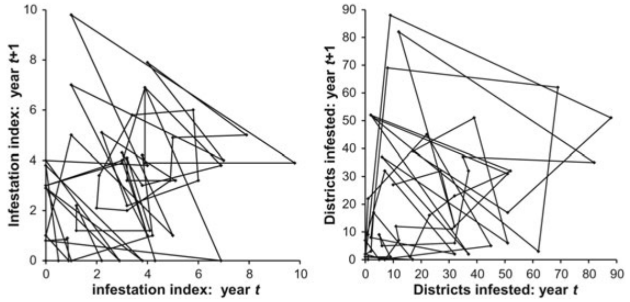

Figure 3. Phase diagrams (see Figure 1 for explanation) for, left, an annual infestation index for the Chinese Migratory Locust *L. migratoria manilensis* for the period 1903–1960 (see Sugihara, 1995; Stige *et al.*, 2007; Tian *et al.*, 2011) and, right, numbers of magisterial districts in Botswana, Namibia, and South Africa infested annually with Brown Locusts *Locustana pardalina* from 1946 to 1997 (data from Tratalos (2001) and Todd *et al.*, 2002).

There is evidence that r for gregarious populations in both desert locusts and the African armyworm is more than r for the corresponding solitarious populations (Cheke, 1978, 1995). Also, the invasion area and hence the carrying capacity (K) of gregarious *phase* insects is greater than that for solitarious, recession, populations (see above). Thus, the models include shifts in both of these parameters. Although the equations which follow can be used for modelling any insect with *phase* change, we based them on the biology of the desert locust, as this is the most studied of the relevant species. Given changes in r associated with *phase* changes in this species, Holt and Cheke (1996) modified model 1 to include an abrupt density-dependent shift in the value of r to mimic a *phase* change from the solitarious to the gregarious condition, which may involve a switch from a non-chaotic to a chaotic value of r. They also extended the model by making K a function both of density and of environmental variation. K for the population of solitarious individuals was assumed to be lower than that for gregarious populations, given the huge differences between the geographical extents of the recession and invasion areas (see above). The transition in the value of K, rather than being abrupt, was assumed to follow a sigmoid curve. Thus, the model became:

$$\begin{cases} x_{t+1} = x_t \exp\left(r_t\left(1-\dfrac{x_t}{K_t}\right)\right) \\ K_t = u + K_s + \dfrac{K_g - K_s}{1+\exp(-a_K(x_t - m_K))} \\ r_t = r_s + \dfrac{r_g - r_s}{1+\exp(-a_r(x_t - m_r))} \end{cases} \tag{2}$$

where K_s is the carrying capacity, solitarious population; K_g the carrying capacity, gregarious population; a_K the transition slope parameter; m_K the transition threshold parameter; r_s the population growth rate, solitarious; r_g the population growth rate, gregarious; a_r the transition slope parameter; m_r the transition threshold parameter; and u is a uniformly distributed random variable with range 0 to δ. Thus, δ represents the intensity of the environmental noise.

Parameterized versions of this model provided realistic output that was similar to time-series of locusts and had similar autocorrelation function (ACF) and partial ACF (PACF) characteristics (ACFs measure the correlation between values at k and at previous lags $k - 1$, $k - 2$ etc.; PACFs measure autocorrelation at lag k that takes account of autocorrelations at lags $<k$; Holt and Cheke, 1996). The model was sensitive to variations in r_g and the latter's value was within the chaotic zone for the logistic map, the duration of plagues was predicted to be shorter and the variance of their lengths reduced when compared with output using lower values of r_g. Holt and Cheke went on to use equations from catastrophe theory to examine the effects of catastrophic shifts in r and

Ibrahim (2001) used the equations for Monte Carlo simulations of a metapopulation model of desert locusts, but none of these authors expanded their models to include the effects of predation and time-lags, the main subjects of this paper.

Models including a predator

Here, we expand model 2 by including predation which has not been accounted for in locust models to date, with only the insects' endogenous dynamics having been considered, apart from a random environmental element. However, Elliott (1962) reported that 100 species of birds from 34 different families were known to attack hoppers and adults of the desert locust. Greathead (1963) listed insect enemies of grasshoppers and locusts worldwide, what is known of natural predators of locusts in the Sahel was summarized by Greathead *et al.* (1994) and Mullié (2009) listed avian predators of locusts and grasshoppers in Africa as a whole. It is likely that if sufficient numbers of predators locate swarms then they may be capable of reducing the insect populations, but the numbers of locusts taken by the predators will be density dependent. Perhaps the most important predator of locusts and armyworm is man (although, unlike natural predators, human populations do not depend on the dynamics of their prey), by deployment of large-scale insecticide operations, but there are also many other vertebrate and invertebrate predators and parasites of locusts (Greathead, 1963; Uvarov, 1977) and armyworm (see Appendix 3, Rose *et al.*, 2000). Furthermore, the hoppers of the desert locust and the Australian plague locust *Chortoicetes terminifera* are often cannibalistic, a form of predation that has been proposed as an additional factor promoting movement as the insects get attacked from behind (Bazazi *et al.*, 2008; Hansen *et al.*, 2011).

If it is assumed that there are y_t predators that attack the locusts according to Holling's disc equation (Holling, 1959), then Equation (2) can be modified to:

$$\begin{cases} x_{t+1} = x_t \exp\left(r_t\left(1-\dfrac{x_t}{K_t}\right)-\dfrac{\alpha T y_t}{1+\alpha T_h x_t}\right) \\ K_t = u + K_s + \dfrac{(K_g - K_s)}{1+\exp(-a_K(x_t-m_K))} \\ r_t = r_s + \dfrac{r_g - r_s}{1+\exp(-a_r(x_t-m_r))} \\ y_{t+1} = x_t\left(1-\exp\left(-\dfrac{\alpha T y_t}{1+\alpha T_h x_t}\right)\right) \end{cases} \tag{3}$$

where T is the searching time (total time prey is exposed to predators), T_h the handling time (time between prey being found and search by predator resumed), and α the instantaneous search rate (average encounters per host per unit of searching time). To compare results with those obtained by Holt and Cheke (1996), we chose the same parameter values that they used for their initial model. That is, $K_s = 0.2$, $K_g = 1$, $m_K = 0.85$, $m_r = 0.85$, $a_K = a_r = 10$, $r_s = 2$, $r_g = 2$ with the intensity of environmental noise $\delta = 0.5$ and the other parameter values in system (3) were fixed as $T = 100$, $T_h = 1$, $\alpha = 0.022$, unless otherwise stated. [Note that Holt and Cheke (1996) stated that values of $a_K = a_r = 0.1$ were used in their simulations, but this was a typographical error, as in fact $a_K = a_r = 10$ were used]. Three different simulations of system (2) and corresponding time-series of system (3) with different values for the instantaneous search rate α are given in Figure 4, with statistics on the output summarized in Table 1. These results show that predation can reduce the average density of prey populations, reduce durations of periods when the populations remain in the gregarious *phase*, and reduce the frequency of population shifts from the solitarious state to the gregarious form. As expected, the effects are more pronounced with increasing values of the instantaneous search rate α, which implies that the predator population may play a pivotal role in controlling the *phase* changes and keeping the prey population in check, although it cannot completely suppress it.

With a different parameter set, there exists a quasi-periodic solution for system (3) with attractors for x_t and y_t without stochastic perturbation, i.e. $\delta = 0$ (Figure 5). Addition of a random environmental noise element ($\delta = 0.3$) alters the attractor such that the quasi-periodic patterns are lost, giving an attractor which resembles phase diagrams of actual locust dynamics (Figure 6). We note that the single-species model (2) does not have attractors of this type, which suggests that the model including predation is more realistic. The general shape of the attractor (e.g. like Figure 6a or more oval) is sensitive to variations in parameter values such as α, K_g, and K_s and, interestingly, is maintained with values of $r_g = 2$ or, even, with $r_g < r_s$. That the system is chaotic even with very low values of r_g is confirmed by a bifurcation analysis for the parameter values given in Figure 7a. With different values of r_g, even more interesting basins of attraction, including quasi-periodic attractors (Figure 7b), multi-point cycles (Figure 7c), and a strange attractor (Figure 7d), can be found with shifts between generations from high density, gregarious, populations to low-density solitarious populations and *vice versa* (Figure 7b–d).

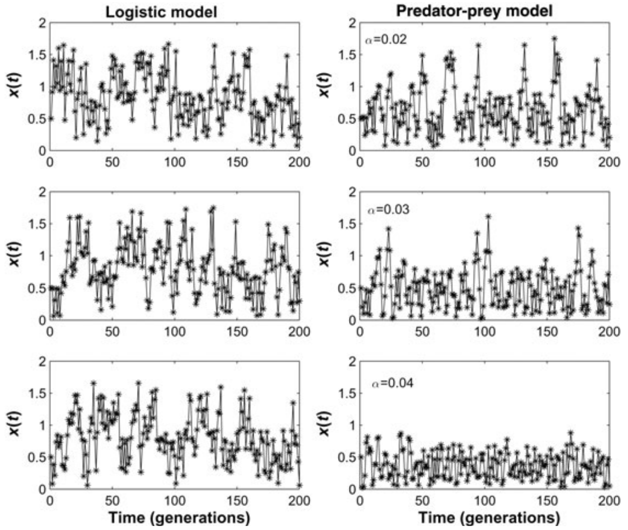

Figure 4. Time-series of densities of insects (x_t) from simulations of model system 2 (logistic model alone, left) and the modified version, system 3, including effects of predation (predator–prey model, right). Parameter values used for both models were as follows: solitarious carrying capacity $K_s = 0.2$, gregarious carrying capacity $K_g = 1$, transition threshold parameter for carrying capacity $m_K = 0.85$, transition threshold parameter for intrinsic rate of increase $m_r = 0.85$, transition slope parameter for carrying capacity $a_K = 10$, transition slope parameter for intrinsic rate of increase $a_r = 10$, solitarious intrinsic rate of increase $r_s = 2$, gregarious intrinsic rate of increase $r_g = 2$, intensity of environmental noise $\delta = 0.5$, and, for system 3, searching time $T = 100$, handling time $T_h = 1$. The same value for u, representing random perturbation, was chosen to simulate both models, i.e. it was fixed for each row. Three different values (0.02, 0.03, and 0.04) for α were used for system (3).

Table 1. Means, variances, maxima, and minima of output from different models and the numbers of generations out of a possible 200 that the insects were in a gregarious phase (Gens.), defined as so when their population densities at time t, $x(t)$, exceeded 0.85, and the numbers of times when there were switches from the solitarious to the gregarious condition (Switches)

Model	Mean	Variance	Maximum	Minimum	Gens.	Switches
Logistic model (Figure 4)	0.74	0.15	1.72	0.05	72	21
Predator – prey model no delay ($\alpha = 0.02$), Figure 4	0.64	0.13	1.71	0.04	47	19
Predator – prey model no delay ($\alpha = 0.03$), Figure 4	0.47	0.09	1.52	0.03	19	7
Predator – prey model no delay ($\alpha = 0.04$), Figure 4	0.36	0.03	0.84	0.02	0	0
Predator – prey model with delay ($\alpha = 0.02$; $\tau = 1$), Figure 9	0.46	0.12	1.38	0.0003	29	29
Predator – prey model with delay ($\alpha = 0.03$; $\tau = 1$), Figure 9	0.44	0.09	1.50	0.003	21	21
Predator – prey model with delay ($\alpha = 0.04$; $\tau = 1$), Figure 9	0.38	0.06	1.30	0.002	5	5

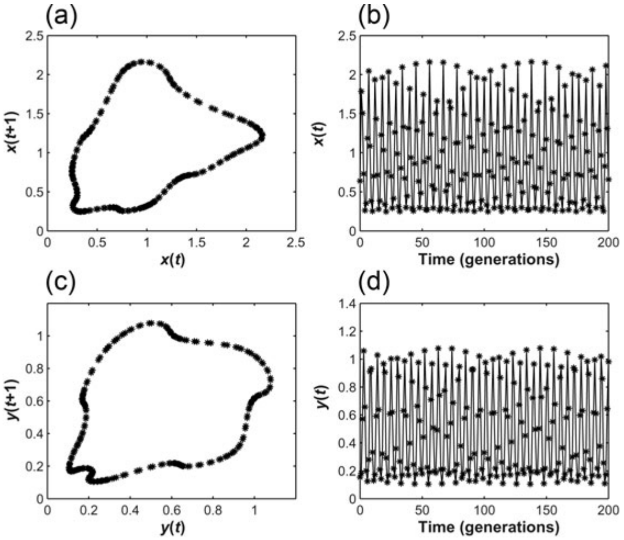

Figure 5. Attractor (a region or set in n-dimensional space towards which a variable, in this case the population density, moves with time as dictated by characteristics of the system, i.e. points that get close to the attractor remain close even if they are slightly perturbed) for system 3, with the following parameter values fixed, $K_s = 2$, $K_g = 5$, $m_K = 3$, $m_r = 3$, $a_K = a_r = 10$, $r_s = 2$, $r_g = 5$, $\alpha = 0.022$, $\delta = 0$, $T = 100$, and $T_h = 1$. δ represents the intensity of the environmental noise. See Figure 4 for an explanation of the other terms. (a) Quasi-periodic solution (i.e. the pattern does not repeat itself exactly, as in a periodic solution) for the prey population, where the density of prey at generation $t + 1$ is plotted against the numbers at t. (b) Time-series of the prey population. (c) Quasi-periodic solution of predator population, where the density of predators at generation $t + 1$ is plotted against the density at t. (d) Time-series of the predator population.

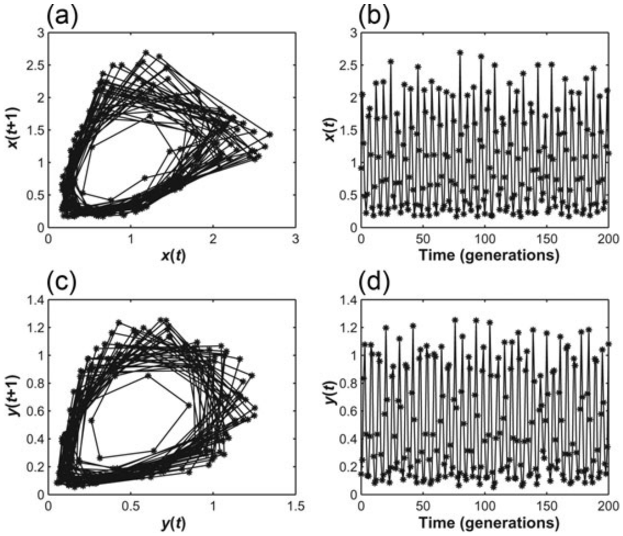

Figure 6. Attractor for the same system as for Figure 5, but with $\delta = 0.3$. (a) Solution of the prey population, where the density of prey at generation $t + 1$ is plotted against the density at t. (b) Time-series of the prey population. (c) Solution of the predator population, where the density of predators at generation $t + 1$ is plotted against the density at t. (d) Time-series of the predator population.

Models with time delays

The Holt and Cheke (1996) models derived from the logistic equation assumed that there was a direct transition from the solitarious to the gregarious *phase*. However, there is an intermediate transient state when the locusts are neither one nor the other. When gregarizing, desert locusts may exhibit gregarious behaviour yet retain solitarious morphology, and it may take two or three generations of remaining at high densities for the full gregarious condition to be reached during a congregating transient *phase*. Thus, there is a delay between the solitarious and gregarious condition when the insects are transitional and this transient *phase* is also passed through in the reverse direction when locusts are reverting to the solitarious condition during a segregating transient period. Thus, Uvarov (1966) wrote that the scheme "results in two reasonably definable extreme *phases*, separated by a more or less long continuous series of transient forms". The *phase* changes, however, exhibit hysteresis insofar as the change from the solitarious *phase* to the gregarious can be much faster than the reverse process. This hysteresis effect was modelled by Holt and Cheke (1996) using a cusp catastrophe function, but this was very sensitive to environmental variation and often led to population collapses when the intrinsic rate of increase became high. To mimic the delays within a logistic framework but without hysteresis, Equations (3) were further modified by assuming delays in the functions defining the carrying capacity (K) and the intrinsic rate of increase (r), thus:

$$\begin{cases} x_{t+1} = x_t \exp\left(r_t\left(1 - \dfrac{x_t}{K_t}\right) - \dfrac{\alpha T y_t}{1 + \alpha T_h x_t}\right) \\ K_t = u + K_s + \dfrac{K_g - K_s}{1 + \exp(-a_K(x_{t-\tau} - m_K))} \\ r_t = r_s + \dfrac{r_g - r_s}{1 + \exp(\,-\,a_r(x_{t-\tau} - m_r))} \\ y_{t+1} = x_t\left(1 - \exp\left(-\dfrac{\alpha T y_t}{1 + \alpha T_h x_t}\right)\right) \end{cases} \tag{4}$$

where τ is the length of the time-lag.

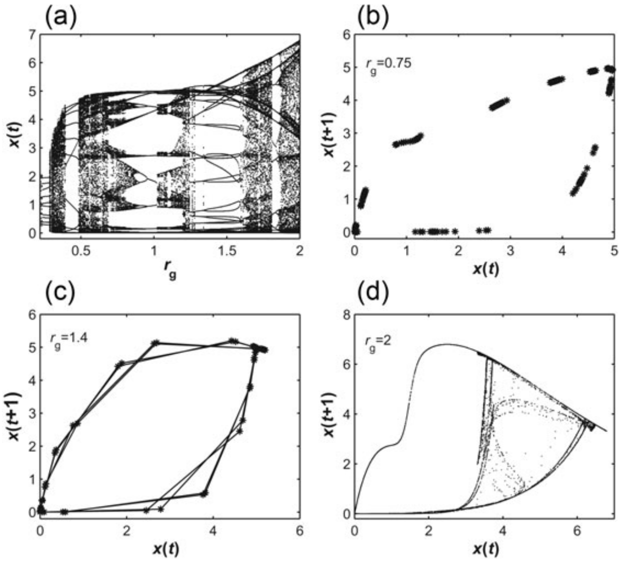

Figure 7. Numerical bifurcation analysis, a method for examining how small changes in one parameter, here r_g, can cause qualitative changes in the behaviour of the system, illustrated here by population density, for system 3 with parameters fixed as follows: $K_s = 2$, $K_g = 5$, $m_K = 1.5$, $m_r = 1.5$, $a_K = a_r = 10$, $r_s = 2$, $\alpha = 0.02$, $\delta = 0$, $T = 100$, and $T_h = 1$. See Figures 4 and 5 for explanations of these terms. (a) Bifurcation diagram with parameter r_g varied from 0.22 to 2. (b) Quasi-periodic attractor at $r_g = 0.75$. (c) Multi-point cycle at $r_g = 1.4$. (c) Strange attractor (i.e. an attractor with fractal structure) at $r_g = 2$.

To investigate how the time delay affects *phase* changes, we first studied the logistic model (2) with and without the time delay included in model (4). From Figure 8, it is clear that the number of generations that the locust population remains in the gregarious *phase* is dramatically decreased as r_g increases and is significantly affected by introduction of the time delay. The latter is confirmed by results of simulations, similar to those depicted in Figure 4, for system (4) with the time delay fixed at $\tau = 1$ (Figure 9, Table 1). Combined with the results shown in Figure 4, we further conclude from the output in Figure 9 that the transient period (time delay) is also instrumental in constraining the prey population within lower bounds, as it reduces the mean, maximum, and minimum values of the prey to lower than the corresponding values apparent in the predator–prey output in Figure 4, except the mean with $\alpha = 0.04$ (Table 1). In addition, models with the time delay constrain the gregarious *phase* to single generations at a time, as the numbers of gregarious generations and of switches are identical (Table 1), which is not realistic. With a different parameter set, the dynamical behaviour of solutions of system (4) includes attractors with a loop in the centre (Figure 10).

Of interest is the case, with $\delta = 0$, of a bifurcation analysis in which bifurcations and chaos result even with very low values of r_g (Figure 11a). Other more interesting attractors for delay models with one- and two-generation time delays and different combinations are obtainable, several examples of which are given in Figure 11b–d, including the remarkable "toy windmill" pattern of Figure 11c. These attractors such as the 20-point and 30-point cycles resemble the phase diagrams of actual locust dynamics based on field data of numbers of geographical units infested (Figures 1–3).

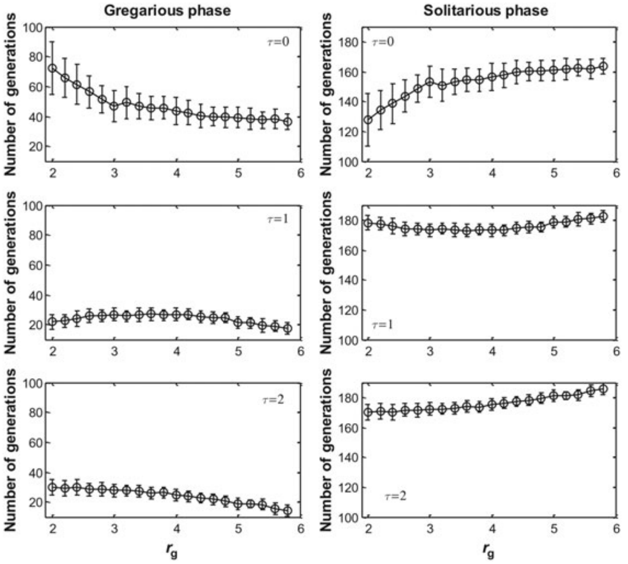

Figure 8. The numbers of generations that populations remain in the gregarious *phase* (left) or solitarious *phase* (right) from simulations of the logistic model with or without time delay. Parameter values are $K_s = 0.2$, $K_g = 1$, $m_K = 0.85$, $m_r = 0.85$, $a_K = a_r = 10$, $r_s = 2$, $\delta = 0.5$, r_g varied from 2 to 5.8 and time delay $\tau = 0$, 1 or 2. See Figures 4 and 5 for explanations of these terms. The mean and variance of 50 simulations with respect to three different time delays (0, 1, or 2) as a function of r_g are plotted. A population was classed as remaining in the gregarious *phase* at generation *i* if $x(i) > 0.85$ at generation *i*, else it switched to and remained in the solitarious *phase*.

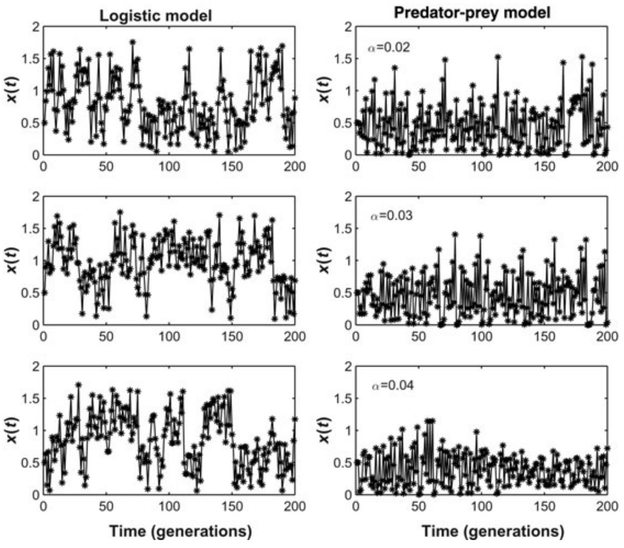

Figure 9. Time-series of densities of insects (x_t) from simulations of systems 2 (logistic model, left) and 4 (predator-prey model with time delay, right). Parameter values for both models were as for Figure 4, i.e. $K_s = 0.2$, $K_g = 1$, $m_K = 0.85$, $m_r = 0.85$, $a_K = a_r = 10$, $r_s = 2$, $r_g = 2$, $\delta = 0.5$ and, for system (4), $T = 100$, $T_h = 1$, $\tau = 1$. See Figures 4, 5, and 8 for explanations of these terms. The same random perturbation was chosen to simulate both models, i.e. it was fixed for each row, but three different values (0.02, 0.03, and 0.04) for α were used for system 4.

Model outputs and empirical data compared

The lack of data on locust densities precludes a direct comparison between empirical data and model outputs, as does the unreliability

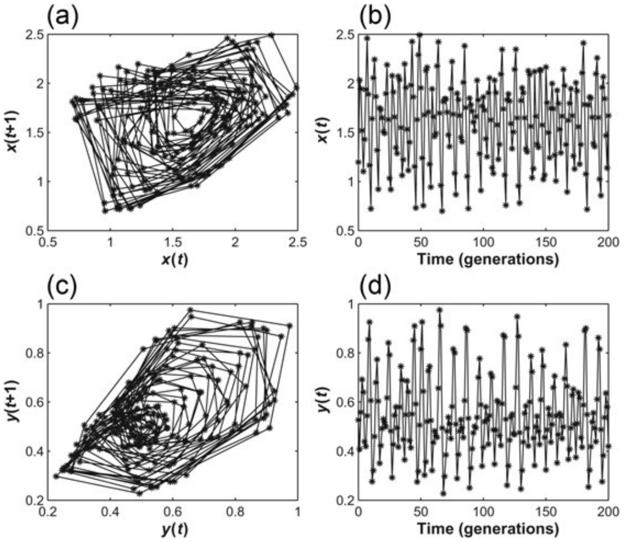

Figure 10. Attractor for system 4 with $K_s = 2$, $K_g = 5$, $m_K = 1.5$, $m_r = 1.5$, $a_K = a_r = 10$, $r_s = 2$, $r_g = 0.3$, $\alpha = 0.008$, $\tau = 1$, $\delta = 0.3$, $T = 100$, and $T_h = 1$. See Figures 4, 5, and 8 for explanations of these terms. (a) Attractor for the prey population, where the densities of prey at generation $t + 1$ are plotted against the densities at t. (b) Time-series of the prey population. (c) Attractor for the predator population, where the densities of predators at generation $t + 1$ are plotted against the densities at t. (d) Time-series of the predator population.

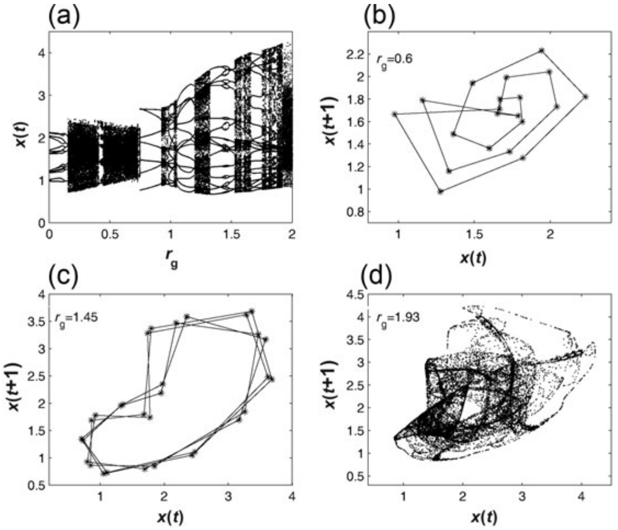

Figure 11. Attractor for system 4, with $K_s = 2$, $K_g = 5$, $m_K = 1.5$, $m_r = 1.5$, $a_K = a_r = 10$, $r_s = 2$, $\alpha = 0.008$, $\tau = 1$, $\delta = 0$, $T = 100$, and $T_h = 1$. See Fgures 4, 5, and 8 for explanations of these terms. (a) Bifurcation diagram with parameter r_g varied from 0 to 2. (b) Twenty-point cycle at $r_g = 0.6$. (c) Thirty-point cycle at $r_g = 1.45$. (c) Strange attractor at $r_g = 1.93$.

of solitarious locust data, but it is possible to compare aspects of model outputs with numbers of territories infested with swarms or numbers of grid squares so infested. A characteristic of both the latter sorts of data are highly significant positive autocorrelation coefficients (PACFs) for lags of 1 time unit for data expressed at intervals of 1, 4 months, or 1 year. Table 2 summarizes such data and compares them with results of PACF analyses of output from different models. These results show that the PACF characteristics of the empirical data are shared by outputs of the logistic model and the predator–prey model without time delays (apart from when $\alpha = 0.04$), but not by models with the delay (for which the first lags are significant but negative).

Discussion

That the dynamics of theoretical populations of insects with *phase* change are non-linear is unsurprising, given the constructs used in the models. It was, however, surprising to find that chaotic solutions were also possible with very low values (<0.25) of the gregarious intrinsic rate of increase (r_g) by including predation (Figure 7a) and delays in the timing of the *phase* shifts (Figure 11a); the classic logistic map does not become chaotic until r exceeds 2.692 (May, 1974). That the systems modelled here can have different system states with realistic characteristics lends confidence to a conclusion that to achieve realism both predation and delays need to be included in future modelling aimed at forecasting with a view to assisting control strategies. Any such forecasting models will need to include rainfall parameters, here subsumed within the environmental noise term, given the reliance of locusts and armyworms on adequate rain in the right places at the right times for their breeding to be successful and the known impact of rainfall on locust population dynamics (Tratalos *et al.*, 2010).

Irrespective of the non-linearities, comparisons between the results of the original model presented by Holt and Cheke (1996) and those given here show that the introduction of a predator and of time delays can still yield realistic results. That no attractor that resembles the phase diagrams of locust data was obtainable from the original model, whereas both modified models did produce such output supports the conclusion that the latter are more realistic, although the PACF analyses imply that the addition of delays does not improve the realism. It is also realistic that increasing the instantaneous predator search rate, α, increases the effect of the predators on the prey in models with and without the time delay. However, our models do not address whether predation will be more or less effective against gregarious than solitarious insects, although this could be achieved in future work by examining effects of variations in the handling time (T_h) as well as α on both *phases*. There is evidence that some predators such as *Stomorhina lunata* and *Sphex aegyptius* may congregate in desert locust swarms and move with them (Greathead, 1963) and if flocks of birds find locust hopper bands they can be devastating, but usually only locally, and large hopper bands or adult swarms are likely to exceed the capacity of vertebrate predators (Uvarov, 1977). Indeed, gregarization may reduce rather than increase predation pressure (Sword *et al.*, 2000; Reynolds *et al.*, 2009).

Some of our results are counter-intuitive insofar as the introduction of predation and time delays would be expected to have damping effects rather than allowing the continuation of chaotic outcomes under some circumstances. Further research to understand the reasons for this result is needed as are additional investigations to include the effects of hysteresis by varying the transition slope and threshold parameters to complement the cusp catastrophe model of Holt and Cheke (1996).

The models assume that a single population is involved but, for the desert locust, and perhaps in other species with *phase* change, it is likely that several subpopulations may respond simultaneously to common environmental signals such as widespread rainfall. If this is so, then a metapopulation approach, also taking account of

Table 2. Significant positive (+) and negative (−) lags from PACFs up to ten lags fitted to time-series of data on the Desert locust and outputs from different models

	PACF Lags									
	1	2	3	4	5	6	7	8	9	10
Desert locust data										
No. of territories annual data (Cheke and Holt, 1993)	+	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
No. of grid squares annual (FAO Swarms data 1930–1999)	+	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
No. of grid squares 4-monthly (FAO Swarms data 1930–1999)	+	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
No. of grid squares monthly (FAO Swarms data 1930–1999)	+	−	+	+	+	N.S.	−	N.S.	+	N.S.
Model outputs										
Logistic model (Figure 4)	+	+	N.S.	N.S.	+	N.S.	N.S.	N.S.	N.S.	N.S.
Predator–prey model no delay ($\alpha = 0.02$), Figure 4	+	−	−	N.S.	N.S.	−	N.S.	N.S.	N.S.	N.S.
Predator–prey model no delay ($\alpha = 0.03$), Figure 4	+	N.S.	N.S.	−	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Predator–prey model no delay ($\alpha = 0.04$), Figure 4	N.S.	−	−	−	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Predator–prey model with delay ($\alpha = 0.02$; $\tau = 1$), Figure 9	−	+	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Predator-–prey model with delay ($\alpha = 0.03$; $\tau = 1$), Figure 9	−	+	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Predator–prey model with delay ($\alpha = 0.04$; $\tau = 1$), Figure 9	−	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S., not significant. The PACF is a measure of autocorrelation at lag k that takes account of autocorrelations at lags $< k$, so significance in the PACF shows relationships not explained simply by earlier time-steps.

migrations and local extinctions, may be more appropriate, as was pointed out and modelled by Ibrahim (2001). He constrained his system such that the onsets of gregarization and recession were synchronized across all of his 100 patches, but output for the system as a whole reproduced bi-stable dynamics and confirmed that metapopulation processes could account for observed genetic diversity in recession populations. It would be instructive to determine if the same result was obtainable with the addition of predation and delay terms.

Non-linearities in the dynamics of the desert locust have long been suspected (Cheke and Holt, 1993, 1996; Holt and Cheke, 1996), but demonstrating this with empirical data has yet to be shown conclusively, partly because no time-series data exist on densities of the insects, only on the numbers of geographical units infested. The same is true for the Chinese populations of the migratory locust *L. migratoria manilensis* (Tsao Chi, 1950; Ma, 1958; Stige *et al.*, 2007; Tian *et al.*, 2011), illustrated and previously analysed by Sugihara (1995); but it is relevant that squared terms were needed to model a 50-year sequence of the Chinese locust dataset (Ma *et al.*, 1965), as also the case for desert locust data (Tratalos *et al.*, 2010). Future research on these species and on the populations of other insects with *phase* change will be needed to establish whether the predictions of the models, in terms of non-linear dynamics, are correct. If the dynamics of insects with *phase* change are chaotic in reality, their population dynamics may never be forecasted accurately, even with the inclusion of accurate rainfall terms within a metapopulation framework. However, the models have applied relevance since the introduction of predation into them reduced the prey densities, compared with output based on models without predation, and suggests that any control measures, natural or artificial or in combination, can be effective in reducing the densities of migrant pests with *phase* change. That time delays reduced the prey even further suggests that measures to inhibit *phase* changes from a solitarious condition to either transient or gregarious states will also be useful control tactics. It is also interesting and worthy of further investigation that increasing r of the gregarious phase did not lead to increased time spent in the gregarious *phase* with or without time delays.

The most significant autocorrelation in analyses of monthly desert locust data (Tratalos *et al.*, 2010) and in analyses of annual data (Cheke and Holt, 1993) was 1, supported by the finding that 12 months was the most significant seasonal moving average process in square-root transformations of the data in Tratalos *et al.* (2010). Thus, it was of special interest that, with a time delay of 1, the value of r_g giving maximal periods in the gregarious *phase* was ~4 (Figure 8), which corresponds to empirical estimates based on field data of 3.96 per generation for populations laying 2 egg-pods per generation (Blackith and Albrecht, 1979) and up to 4.8 per generation for populations laying 3 egg-pods (Cheke, 1978; Blackith and Albrecht, 1979; Cheke and Holt, 1993).

In conclusion, the results support the idea that locust dynamics are non-linear and may be chaotic and show that inclusion of time delays and predation into population models reveal general patterns consistent with field data. These conclusions have implications for modelling in support of control strategies and may, perhaps, have parallels in understanding the fluctuations of exploited fish populations that are polyphenic, be they freshwater, marine, or anadromous species. However, the models presented here are discrete time difference equations and it would be valuable to explore other approaches such as continuous time differential equation expressions or models taking greater account of hysteresis, spatio-temporal variability, intraspecific competition, dispersal, environmental structure, and extra trophic levels. Such models might yield different conclusions about the dynamics of insects with phase change.

Acknowledgements

We are very grateful to Dr Joyce I. Magor for giving us access to an updated version of the FAO SWARMS dataset and to Dr Howard Browman and three referees for their constructive suggestions which prompted significant improvements to the paper.

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Handling editor: Howard Browman

ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(8), 2231–2241. doi:10.1093/icesjms/fst189

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Environmental and fishery-driven dynamics of the common octopus (*Octopus vulgaris*) based on time-series analyses from leeward Algarve, southern Portugal

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Sonderblohm, C. P., Pereira, J., and Erzini, K. Environmental and fishery-driven dynamics of the common octopus (*Octopus vulgaris*) based on time-series analyses from leeward Algarve, southern Portugal. – ICES Journal of Marine Science, 71: 2231–2241.

Received 1 July 2013; accepted 12 October 2013; advance access publication 11 January 2014.

Dynamic factor analysis was used to explore monthly landings per unit effort (LPUE) series of *Octopus vulgaris* and environmental variables recorded in the southwest Iberian Peninsula, south Portugal. Despite the large fluctuations in the octopus abundance series, results showed a strong aggregation pattern for the last 3 months of the year, possibly related to the input of new recruits to the fishery. The calculated common trend for the 12 months time-series presented significant correlations with autumn rainfall of the previous year (lag − 1), particularly for the October, November, and December series. Other important correlations were found for the Western Mediterranean Oscillation index (lag − 1), Ekman transport, summer river run-off (lag − 1), horizontal and vertical component of windstress, among others. The main trend describes a moderate steady increase in LPUE during the last 10 years, suggesting that octopus abundance has increased from 1990 to 2010. The strong correlations of the monthly octopus LPUE series, together with the annual life cycle, suggest that after environmentally controlled recruitment, population dynamics is largely fishery driven, resulting in strong seasonality in the landings.

Keywords: environment, *Octopus vulgaris*, Portugal, recruitment, time-series, trap fishing, trends.

Introduction

Cephalopod populations are well known to exhibit wide fluctuations in abundance, mainly due to the presence of a planktonic larval stage particularly sensitive to environmental factors (Pierce *et al.*, 2010). Among them, *Octopus vulgaris* is a short-lived species, with a cycle of around 12–14 months characterized by non-overlapping generations, with only one or two cohorts present in the fishery at any time, and a very rapid growth with high fecundity rates (Pierce and Guerra, 1994). The success of mating, incubation, spawning, paralarval stage, and recruitment to the benthic life are key processes of the octopus life cycle. Identification of the spatio-temporal scale of these events and their relationships with the environment has been the pursuit of many scientists attempting to understand the dynamics of this important mollusc (Payne *et al.*, 2006).

Several studies have tried to identify possible mechanisms that could explain the variability of the recruitment of short-lived marine species in relation to the environment using time-series analyses. Recently, Santos *et al.* (2012) analysed recruitment variability of the Iberian sardine (*Sardina pilchardus*) in relation to environmental parameters using dynamic factor analysis (DFA) and generalized additive modelling (GAM). Another interesting approach was carried out by Lloret *et al.* (2001) who found links between the recruitment of Mediterranean species and local and global environmental conditions based on analyses of cpue data. Thus, the use of environmental variables to examine trends in the abundance of certain cephalopods has received increased interest over the past few years. Robin and Denis (1999) explored the relationships between water temperature and squid abundance in the English channel using time-series analyses. Agnew *et al.* (2000) reported effects of sea surface temperature (SST) on the recruitment of *Loligo gahi* around the Falkland Islands. Zuur and Pierce (2004), Chen *et al.* (2006), and Chen (2010) investigated common trends in Northeast Atlantic squid series using DFA.

Studies on the recruitment of *O. vulgaris* based on fishery data are scarce. Sobrino *et al.* (2002) analysed landings per unit effort (LPUE) of *Sepia officinalis* and *O. vulgaris* in the Gulf of Cadiz using multivariate analyses, showing the influence of rainfall, river discharges, and temperature on the LPUE series. Faure *et al.* (2000) applied the linear regression model and the GAM to relate recruitment indices and environmental conditions in Mauritanian waters, whereas Otero *et al.* (2008) inferred the influence of upwelling events on the recruitment of *O. vulgaris* based on octopus fishery and environmental data.

Santa Luzia, located in the Algarve region (south Portugal), is the most important octopus fishing harbour for the area, yielding an average annual catch of 1300 t during the past two decades (1990–2010). Its fishing fleet has been using a single octopus gear, the octopus trap, for more than 20 years, and landings are sold at auction in the village. Discards represent less than 16% of the catches in weight for this fishery, consisting mainly of small individuals (Baeta, 2009). Hence, as fishing effort is known, LPUE can be estimated from octopus landings recorded in the auction and can be considered a good proxy of the abundance of *O. vulgaris* for the area. Whereas other octopus recruitment studies are based on catching paralarvae or collecting data on very small individuals (Moreno *et al.*, 2008), usually involving long-term sampling surveys, time-series analysis of fisheries data is an alternative approach that could shed light on the population dynamics of this valuable resource in budget limited conditions.

Statistical tools developed for short, non-stationary time-series were used to study the variations in the abundance of *O. vulgaris* and the recruitment dynamics in the south of Portugal. DFA has been successfully applied to fisheries data in recent years (Zuur *et al.*, 2003; Zuur and Pierce, 2004; Erzini, 2005; Erzini *et al.*, 2005; Devine and Haedrich, 2011) with the main goal of finding common trends within the multiple time-series and to explore the relationships and interactions of these trends with explanatory environmental and fisheries variables. This technique, which is basically a smoothing method, can provide key information hidden within time-series and can incorporate explanatory variables. Despite the large fluctuations in the octopus abundance series, where a smoothing technique might not be considered appropriate, the use of DFA as an exploratory technique presents consistent results confirmed by other multivariate techniques, such as principal component analysis (PCoA), clustering and non-metrical multidimensional scaling (NMDS). Here, DFA was used to estimate common trends for *O. vulgaris* LPUE time-series in the leeward Algarve region (southern Portugal), to explore the effects of local environmental variables and their different seasonal combinations on the LPUE time-series, and to gain insight on octopus recruitment.

Material and methods

Fishing grounds

The fishing grounds cover an area of ~750 km^2, mostly composed of soft bottoms (sandy and sandy gravel) off the Algarve leeward coast, the northwest boundary of the Gulf of Cadiz (Figure 1). This transition zone, between the Atlantic and Mediterranean, receives the outflow of the fourth longest river of the Iberian peninsula, the Guadiana river, and some other small rivers flowing from Portugal and Spain. The fleet operates between 1 and 6 nm from the coast most of the year, and most of the catches are still landed in the Santa Luzia Fish Auction of Docapesca, inside the Ria Formosa lagoon, where the local harbour is located.

Local climate

The Algarve region is characterized by a Mediterranean climate (Csb or Csa according to Köppen's classification; Arnaud-Fassetta *et al.*, 2006). The hydrological year starts in October, with most of the rainfall occurring during autumn (average 129 mm). The most intense and frequent winds in the area come from the west and southwest, especially during winter (Martin-Vide and Lopez-Bustins, 2006). East and southeast winds are also quite frequent, especially in summer when the *Levante* blows (Newton and Mudge, 2003). The physical oceanography of this part of the Atlantic is dominated mostly by the Gulf of Cadiz system, where the Mediterranean inflow–outflow plays a strong role (Peliz *et al.*, 2009), but the influence of Atlantic waters from the west persists during the whole year, with intermittent upwelling and relaxation episodes, specially for summer, when these events became more intense and frequent (Relvas, 2002).

Response variable

Official landings statistics for the period 1990–2010 were compiled from the Portuguese Institute for the Sea and Atmosphere (Portuguese acronym: IPMA). This dataset contains monthly landings of *O. vulgaris* by boat from 1990 to 2010, recorded at the "first

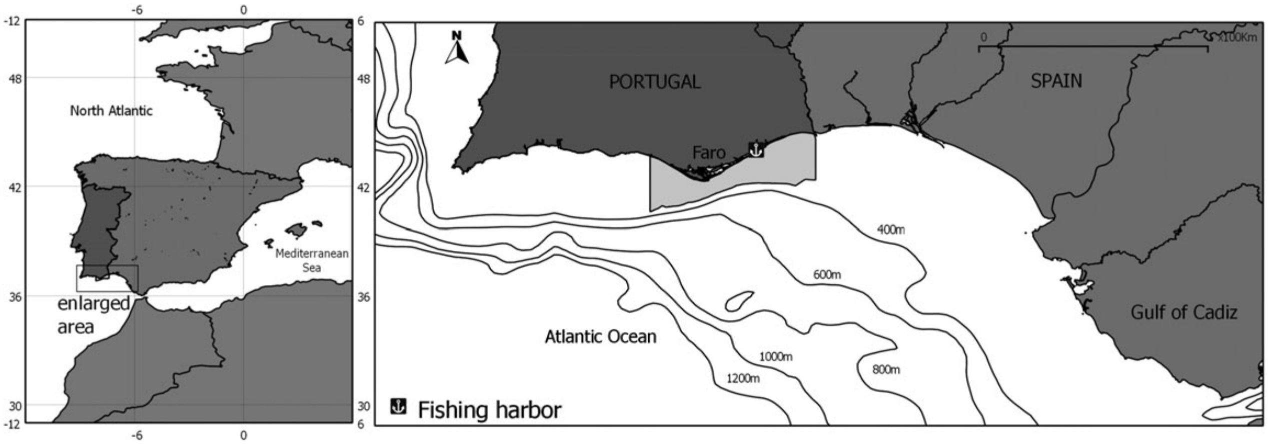

Figure 1. Location of the fishing grounds (grey filled rectangle) (GCS WGS84, projection transv. Mercator).

Table 1. Explanatory variables names, abbreviations, units, and sources used in the analyses.

Abbreviation	Variable name	Description	Unit	Source
Rain	RainFall	Total precipitation by year	Mm	http://snirh.pt/index.php/
River	River discharge	Guadiana river flow measured at Pulo de Lobo Station	m^3s	CIMA Algarve University
SST	Sea surface temperature	Sea surface temperature year average from AVHRR	°C	http://oceanwatch.pfeg.noaa.gov
Ekman	Ekman transport	East–west component of Ekman transport	kg m	http://www.pfeg.noaa.gov
WS_u	Windstress *u* component	*u*-component of pseudostress at 10 m	$m^2 s^{-1}$	http://podaac.jpl.nasa.gov
WS_v	Windstress *v* component	*v*-component of pseudostress at 10 m	$m^2 s^{-1}$	http://podaac.jpl.nasa.gov
GC_z	Zonal geo-current	*z*-component of geostrofic current	$m^2 s^{-1}$	http://oceanwatch.pfeg.noaa.gov
GC_m	Meridional geo-current	*m*-component of geostrofic current	$m s^{-1}$	http://oceanwatch.pfeg.noaa.gov
WeMOi	Western Mediterranean Oscilation Index	Difference between the surface pressures at Cadiz and Padua	Atm	http://www.ub.edu

sale" in the fish auction for every harbour in the Algarve region. To analyse octopus abundance, LPUE was calculated for Santa Luzia, under the assumption that each fishing landing event at the fishing auction represents a fishing day, where LPUE is a simple division of the total landed in a month by boat (kg) by the number of days recorded at auction per month (days):

$$\mathrm{LPUE} = \frac{\mathrm{kg}\ (\text{total of kilos landed by boat in a month})}{\mathrm{days}\ (\text{total of auction days per boat in a month})}.$$

According to Pierce and Guerra (1994), the examination of the correlation between landings, overall effort (landing fishing days), and the resulting LPUE is a useful tool to examine the reliability of LPUE as an abundance measurement. Correlations between landings, effort, and LPUE were analysed and a monthly LPUE time-series dataset was built for the Santa Luzia fleet.

Explanatory variables

In all, nine environmental variables were collected for use in the analysis (Table 1). Following the protocol proposed by Zuur *et al.* (2010), these variables were explored for colinearity, outliers, and missing data before their use in the analysis and modelling. Relationships between the response, LPUE, and the explanatory variables were studied using the Pearson correlation and cross correlations at different time-lags (1, 2 years), given that *O. vulgaris* has a short life cycle (~1 year), with only 1–2 generations generally present in the fishery at any time (Mangold and Von Boletzky, 1973). To explore seasonal variability, 14 combinations for each explanatory variable were created according to the season of the year and its 1-year lagged value (Table 2). These categorical groupings for each variable were based on monthly averages, except for rainfall, where the sums of the values of each month per season were calculated.

Data analysis

LPUE data were log-transformed as suggested by the analysis of the QQ plots of the original data. To facilitate visualization and interpretation, the 12 LPUE time-series and the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation). Analysis of variance was used to test for differences between seasons in effort (landings events), LPUE, and landings, using monthly data grouped into spring, summer, autumn, and winter. A second classification according to the beginning of the hydrological year (October) into rainy and dry seasons was also considered.

Table 2. Different variable combinations and nomenclature used in the analyses (combinations were based on averages by season, except for rainfall, where sums were estimated).

N	Combination	Description	Nomenclature
1	Normal	Normal time-series	var.name
2	Lagged^{-1}	Lagged 1 year	var.name
3	Spring	January, February, March	spr_var.name
4	Summer	April, May, June	sum_var.name
5	Autumn	July, August, September	aut_var.name
6	Winter	October, November, December	win_var.name
7	Rainy season	October–March	rai_var.name
8	Dry season	April–September	dry_var.name
9	Spring^{-1}	Lagged 1 year	spr_var.name^{-1}
10	Summer^{-1}	Lagged 1 year	sum_var.name^{-1}
11	Fall^{-1}	Lagged 1 year	aut_var.name^{-1}
12	Winter^{-1}	Lagged 1 year	win_var.name^{-1}
13	Rainy season^{-1}	Lagged 1 year	rai_var.name^{-1}
14	Dry season^{-1}	Lagged 1 year	dry_var.name^{-1}

Three multivariate techniques were used to explore the 12 monthly LPUE time-series: NMDS, with the Euclidean distance to measure the association between the variables and build the distance matrix D, hierarchical clustering, and PCoA using the covariance matrix and the distance biplot.

DFA is a method to estimate common trends (Zuur *et al.*, 2007) and to investigate which of the monthly time-series follow a common pattern over time that allows incorporation of explanatory variables. A detailed statistical description of DFA is given in Zuur *et al.* (2003). The approach proposed by Zuur and Pierce (2004) was followed, where LPUE data were grouped into 12 time-series, one for each month of the year and modelled as a function of linear combinations of common trends, a constant level parameter, one or more explanatory variables and a noise term:

$$N\ \text{time - series} = \text{constant} + \text{linear combination of } M \text{ common trends} + \text{explanatory variables} + \text{noise}.$$

Three sets of DFA models were fitted in a stepwise method, using symmetric non-diagonal and diagonal matrices (Table 3). Akaike's information criterion (AIC) was used as a measure of goodness of fit to compare the models (Zuur *et al.*, 2003), whereas factor loadings and canonical correlations were used to measure the relation of a particular trend with the time-series. For the first group, the *N* time-series were modelled as a linear combination of *M* common trends, without explanatory variables.

In the second set, explanatory variables and their combinations were added one by one to the best models obtained from the first set for both types of error covariance matrices. This stepwise procedure allowed the relative importance of each variable to be identified based on the AIC, as well as the *t*-values for the individual regressions for each time-series. For the third set, the best model from the first set with one common trend (symmetric non-diagonal matrix) was selected and the most important explanatory variable combinations obtained from the second set were incorporated. Models with two and three explanatory variables were fitted.

Results

Octopus landings showed great variability and seasonality, oscillating between 7 t in September 1990 and 250 t in November 2007 (Figure 2), with an average of 45 t (s.d. = 35) per month. A strong relationship was found between landings and the estimated LPUE (Pearson correlation = 0.90). Since there were no landings in August 2005 due to a voluntary fishing ban, the missing value in the time-series was replaced by the mean LPUE of the months of August (46.3 kg day vessel^{-1}).

Table 3. DFA set used in the analyses.

Set	Model	Covariance matrix *R*
1	12 time-series = constant + *M* common trend + noise	Diagonal
	12 time-series = constant + *M* common trend + noise	Non-diagonal
2	12 time-series = constant + *M* common trend + one explan. var. + noise	Diagonal
	12 time-series = constant + *M* common trend + one explan. var. + noise	Non-diagonal
3	12 time-series = constant + *M* common trend + two or three explan. var. + noise	Non-diagonal

LPUE by season of the year shows evidence of differences in relative abundance, with winter (January–March) having the highest mean LPUE (78.6 kg day vessel^{-1}; s.d. = 33.5; $p < 0.05$; Figure 3). Based on the hydrological classification, LPUE in the rainy period (73.6 kg day vessel^{-1}; s.d. = 34) is higher than in the dry period (58.4 kg day vessel^{-1}; s.d. = 24; $p < 0.001$; Figure 3). Furthermore, LPUE has increased over the years, from an average of 56 kg day vessel^{-1} (s.d. = 26) for the first half of the series (1990–1999) to a significantly higher average 74 kg day vessel^{-1} (s.d. = 33) for the second half (2000–2010) ($p < 0.05$). Moreover, landings events (considered as the effort measurement for LPUE) showed no differences by season or year ($p > 0.05$).

The log-transformed and standardized LPUE monthly time-series are shown in Figure 4. PCoA, hierarchical clustering, and MDS (not shown) gave similar results, with a clear separation of autumn months (October–December) from the other months. PCoA of the monthly LPUE data, based on the covariance matrix, explained 76% of the variability, where the first axis seems to be determined by the first 7 months of the year, and the second axis by autumn months (October–December). The sequential arrangement of the variables on the biplot suggests a monthly correlation, where LPUEs of consecutive months tend to be strongly correlated (Pearson correlation = 0.80). However, within the 20 years sampled, these correlations between the LPUE monthly vectors are less well represented in some years (e.g. 1990, 1991, 1993, 1997, 1998).

For the first set of DFA models, without explanatory variables, the best fit was for model 4a with four common trends plus noise with a symmetrical non-diagonal matrix (Table 4). However, model 1b with one common trend and a non-diagonal symmetric matrix had a lower AIC value (AIC = 448), but higher diagonal elements of the error covariance matrix (average error = 0.80). The

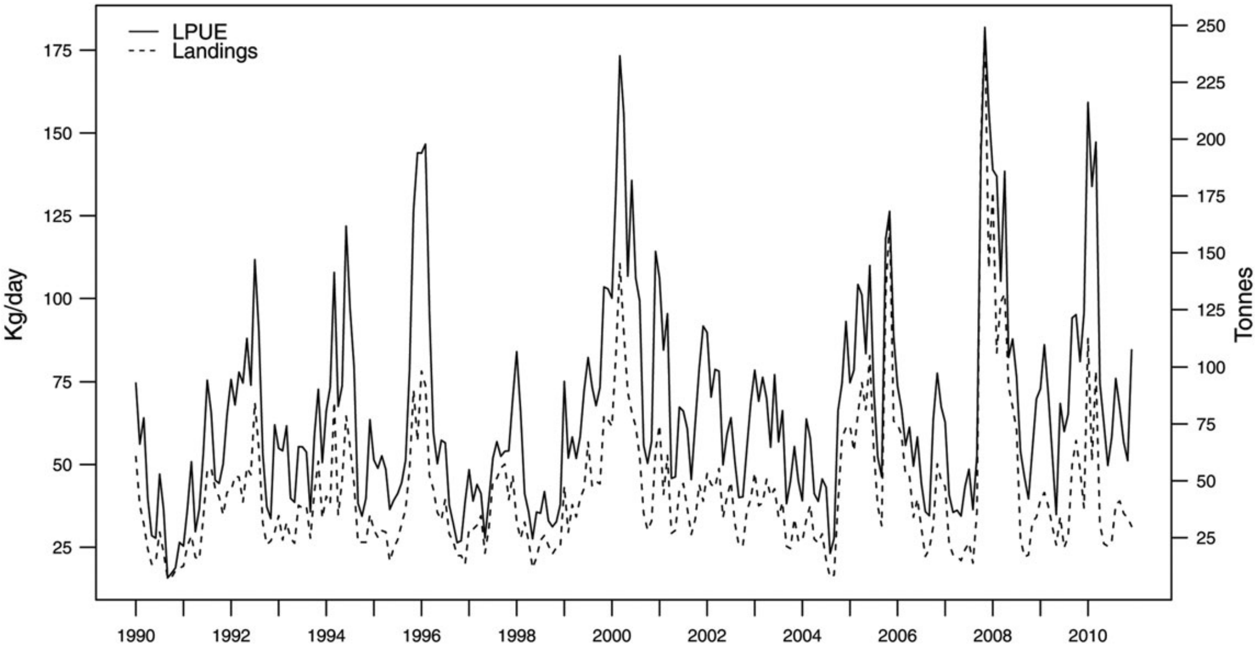

Figure 2. *Octopus vulgaris* monthly landings (tonnes) and estimated LPUE (kg d^{-1}) from Santa Luzia harbour between 1990 and 2010. Data compiled from the Portuguese Institute for The Sea and Atmosphere (IPMA) recorded at the "first sale" in the fish auction.

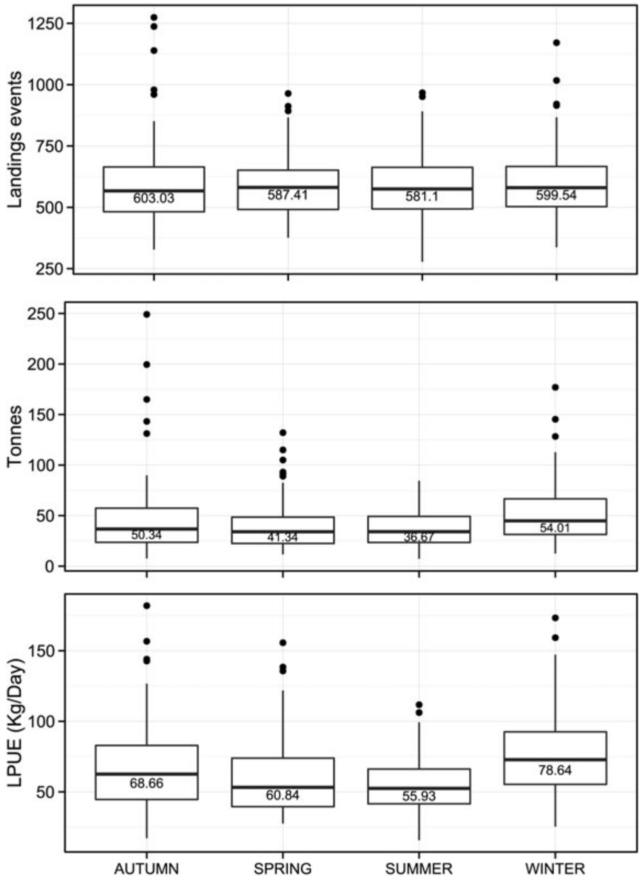

Figure 3. Box plots of Effort (fishing landings events), Landings (tonnes), and LPUE of *O. vulgaris* by season (spring, summer, winter, and autumn). Numbers in the box represent averages, and the horizontal line is the median. The hydrological year start in autumn (October), which is the beginning of the rainy season.

plot of the observed vs. fitted values of the 12 LPUE time-series for model 1b showed poor fits for the first 8 months, improving for September–December. The inspection of the diagonal elements of the error covariance matrix showed that model 4a had very small values for months 2, 5, 7, 9, 10, and 11, especially for months 2 and 9, which resulted in perfect fits, whereas model 1b registered larger values (Table 5).

For the second set of models, with one explanatory variable included, one common trend and a non-diagonal matrix, autumn rainfall (lag − 1) resulted in a smaller AIC (AIC = 403; model 1b; Table 6), improving the fit of the model by reducing the diagonal elements of the error covariance matrix, especially for autumn months (Table 5). Arranged by the AIC value (increasing order), the five most important variables after rainfall, were: rainy season Western Mediterranean Oscillation index (WeMOi) (lag − 1) with AIC = 429, rainy season Ekman transport with no lags (AIC = 432), horizontal and vertical component of windstress for rainy season (lag − 1) with AIC = 435 and AIC = 437, respectively, and summer river run-off (lag − 1) with AIC = 438.

For the third set of models, with one common trend and more than one explanatory variable, model no. 40 was chosen as the best model. This model had the lowest AIC (AIC = 335; Table 7), resulting from the combination of the rainy season value of Rainfall (lag − 1) and WeMOi (lag − 1) with the summer river run-off (lag − 1). Among the ten environmental indices used, nine resulted in marked drops in AIC when included in the analyses, with eight of the variables associated with important decreases in AIC when lagged 1 year (lag − 1), and five of them were variables corresponding to rainy months.

The calculated *t*-values for the individual regressions for each LPUE series with the environmental variables showed autumn rainfall (lag − 1) had high negative *t*-values for the last 8 months of the year (May–December), with the largest value for September ($t = -7.2$). The rainy season average of vertical component of windstress (lag − 1) and WeMOi (lag − 1) indicated large absolute *t*-values for months 8–12 with a positive relationship between WeMOi and the LPUE series. The dry season average SST (lag − 1) had the largest negative values for spring months.

The factor loadings for DFA model no. 40 show significant positive correlations for 8 months, with negative correlations only for July and August. Months from September to January recorded the highest correlations with the common trend, with the highest values for October and November (canonical correlation >0.5; Figure 5).

Figure 6 shows the observed and fitted LPUE series for model no. 40. For all months, the model adequately fits the data, despite strong inter annual variability. Residuals were evenly distributed for all months, except August and September, where a strong oscillating pattern was found. Figure 7 shows the MDS ordination of the error covariance matrix R for model no. 40 after transformation into a dissimilarity matrix by using absolute correlations. The first axis shows the differences between months, separating them into three main groups: January–August, September, and October–December. Within the first group, it is possible to identify a small subgroup with 2 months: July and August. The trend calculated for model no. 40 is given in Figure 8.

Discussion

Despite the large fluctuations in the octopus abundance series, where a smoothing technique might perhaps not be considered appropriate, the use of DFA as an exploratory technique gave consistent results confirmed by other multivariate techniques, such as PCoA, hierarchical clustering, and NMDS. The three multivariate techniques along with DFA showed the same aggregation pattern for the last 3 months of the year and the fits of the DFA models are quite good, especially for October, November, and December. The analyses of the canonical correlations, as a measure of association between the original time-series and the estimated trend, indicated that the estimated trend is significant for the last three series, October, November, and December. Inspection of the off-diagonal elements of the covariance matrix R confirms this clear grouping (Zuur *et al.*, 2003), indicating two joint interactions: autumn and winter–spring. These groups share a certain amount of information which is partially explained by this common trend, whereas August and September are less clear.

The main trend describes a steep rise in LPUE for the first quarter of the series, followed by a short drop for a couple of years then a moderate and steady increase to the end of the series (Figure 8). In a global analysis, Caddy and Rodhouse (1998) reported that cephalopod landings had increased in recent years in contrast to decreasing groundfish abundance. They argued that fishing pressure has changed ecological conditions in the fishing grounds, where predatory fish have declined and cephalopod stocks have increased. Erzini (2005) also described declines in common trends for at least four of

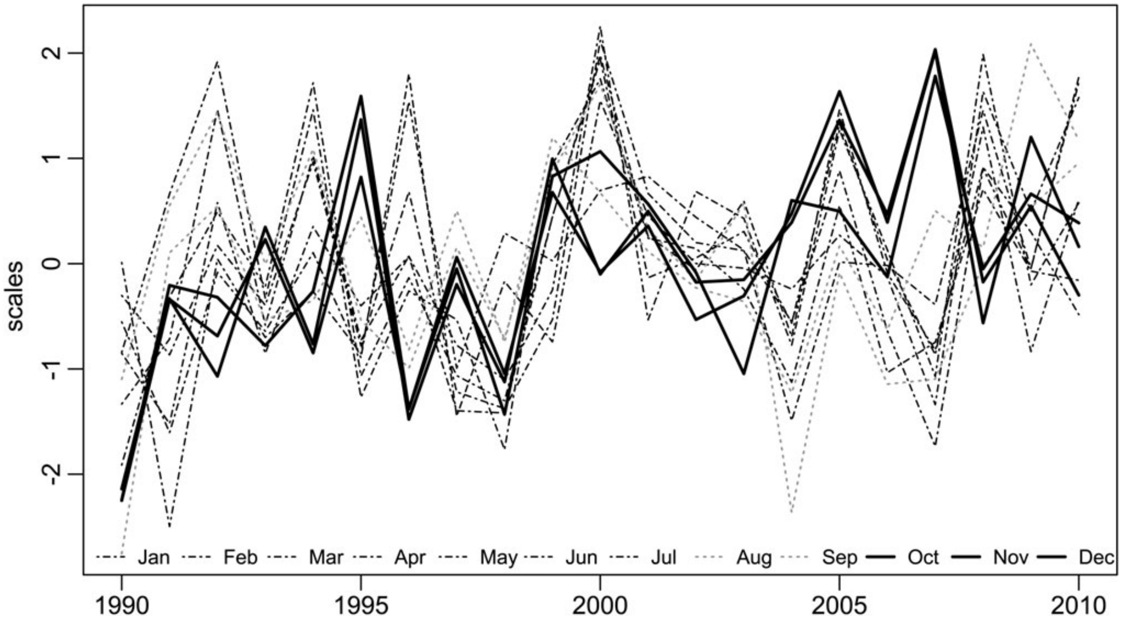

Figure 4. Log-transformed and standardized series of the 12 months LPUE between 1990 and 2010. October, November, and December represented in bold line.

Table 4. AIC values for the first set of DFA models with 1–5 trends and diagonal or symmetric non-diagonal matrix.

Diagonal			**Non-diagonal (symmetric)**		
Model	**Trends**	**AIC**	**Model**	**Trends**	**AIC**
1a	1	624.24	1b	1	448.21
2a	2	551.36	2b	2	455.08
3a	3	519.83	3b	3	472.70
4a	4	500.58	4b	4	492.08
5a	5	506.03	5b	5	508.98

the main commercial finfish species for South Portugal (Algarve) over the past several decades. The rapid stock turnover of *O. vulgaris*, considered an opportunistic species, together with a decline in large predatory demersal fish could be one of the factors contributing to the observed trends in octopus landings. In the report of the Working Group on Cephalopod Fisheries for the Gulf of Cadiz area (ICES, 2012), cpue of *O. vulgaris* presented a very similar trend for some years (1993–2010), with coinciding maxima and minima, except for the last 2 years, where they reported an important drop, especially for 2010. However, the WGCEPH has warned about spatial and temporal constraints of these data, which may potentially bias the comparison.

The increasing trend obtained by the DFA could also be explained, in part, by the increasing numbers of octopus traps. For south Portugal, the number of traps per set increased from 600 units in 2003 (Fonseca, 2003) to 1200 in 2013 (personal observation). This increase has lead to double the amount of bait used, mainly consisting of small pelagics (e.g. *Scombrus japonicus* and *Trachurus trachurus*). Interestingly, studies on lobster traps carried out in the Gulf of Maine (east coast of north America) conducted by Grabowski *et al.* (2010) and Saila *et al.* (2002), and in western Australia by Waddington and Meeuwig (2009) concluded that lobster trap bait, mostly constituted by pelagic fish such as herring, represented a significant food subsidy which contributed to unprecedented increases in lobster abundance. On the other hand, trap losses could also be considered as important substrates for octopus egg-laying and as shelter, and large numbers of lost traps and pots of different sizes and materials are known to litter the bottom in this area (Erzini, 2007). Furthermore, the existence of a bottom trawling exclusion zone, up to 6 nm off the coast where octopus fishing takes place, also provides additional shelter for octopus, thereby enhancing the natural carrying capacity of the ecosystem.

It is well known by the fishers that *O. vulgaris* landings for this area have a marked seasonality, with highest landings generally in winter and lowest in summer, in agreement with the two joint interactions found by the DFA (autumn and winter–spring). Sobrino *et al.* (2011) suggested that the octopus presents an annual life cycle in the nearby Gulf of Cadiz, with recruitment in late autumn and early spring and the reproduction season between July and October. Therefore, we hypothesize that the peak in octopus abundance in winter, from October to December, represents the main recruitment to the fishery, whereas the landings in the consecutive months (January–March) correspond to a second recruitment peak, some late developing individuals, and remaining biomass not fished from previous months. However, the magnitude and timing of the recruitment is highly dependent on external factors, mostly environmental conditions during the paralarval stage.

Moreno (2008) found that there are two main *O. vulgaris* paralarvae peaks, in autumn and spring, in the Portuguese south coast, with the most important peak corresponding to eggs laid at the end of the summer spawning season. The different environmental conditions and geographical features between the northwest coast and the south coast (Algarve) of Portugal result in different timings for spawning peaks of *O. vulgaris*. The northwest population spawns from March to July, in synchrony with the northwest coast upwelling

Table 5. Diagonal elements of the error covariance matrix comparison of the different DFA's set.

Time-series	First set Diag. *M4a*	 No Diag. *M1b*	Second set No Diag. *M1b**	Third set No Diag. *M40*
1	0.31	0.82	0.79	0.67
2	0.00	0.84	0.84	0.59
3	0.08	0.95	0.90	0.64
4	0.20	0.84	0.77	0.64
5	0.09	0.93	0.64	0.59
6	0.08	0.88	0.57	0.49
7	0.08	0.92	0.46	0.44
8	0.09	0.91	0.48	0.43
9	0.00	0.75	0.26	0.25
10	0.04	0.60	0.42	0.33
11	0.03	0.61	0.45	0.36
12	0.19	0.70	0.42	0.29

*M1b**= Model *1b* + autRain^{-1}.

season, whereas the south coast population spawns mainly in summer, between August and September (Lourenço *et al.*, 2012). This spawning pattern is similar to that off NW Africa, in the Arguin Bank and the south Senegalese coast (Demarcq and Faure, 2000). There is, however, no evidence of a genetic structure suggestive of different stocks for this area of the Atlantic (Cabranes *et al.*, 2008).

Among the environmental factors examined, rainfall in late summer and in autumn is one of the most important variables influencing octopus recruitment. It is well documented worldwide that river run-off and rainfall have detrimental effects on the survival of *O. vulgaris* paralarvae (Pierce *et al.*, 2010). In the neighbouring Gulf of Cadiz, Sobrino *et al.* (2002) reported a significant negative correlation between octopus landings and rainfall from the previous hydrological year. In the present study, models with autumn rainfall (beginning of the hydrological year) had the lowest AIC value in the common trend analyses, suggesting a strong correlation between precipitation during the months of October to December and LPUE. Hence, assuming that autumn LPUE is a proxy for recruitment, autumn rainfall from the previous hydrological year is likely the most important factor driving octopus landings in the south of Portugal.

Under the assumption that rainfall affects the survival of paralarvae, the autumn hatching peak found by Moreno *et al.* (2008) is synchronized with the beginning of the rainy season. Based on data available from studies of development in captivity (Iglesias *et al.*, 2004; Cabranes *et al.*, 2008), paralarvae will stay in the plankton for ~40 d, after which they will settle to the bottom and grow to 750 g in 4 months more. Under captive conditions, peak recruitment in October consisting of 600–750 g individuals might stem from spawning having taken place in April of the same year. This could indicate that the secondary maturity peak of March/April in the Algarve and/or the paralarval peak recorded soon thereafter are actually responsible for the vast majority of the landings in the region. However, captive conditions could shorten development significantly, as octopus are very adaptable, and culture conditions may improve the feeding regime and provide more stable and relatively higher than natural temperatures for development. We therefore contrarily propose that the paralarvae of the autumn peak recruit to the fishery ~1 year later, during the next autumn. This is supported by the good fits obtained using environmental variables lagged by 1 year.

Table 6. AIC values for the second set of DFA models with explanatory variables (four trend diagonal and one trend symmetric non-diagonal matrix).

Variable	Error	N	Year (t)	t^{-1}	Wi	Sp	Su	Au	Ra	Dr	Wi t^{-1}	Sp t^{-1}	Su t^{-1}	Au t^{-1}	Ra t^{-1}	Dr t^{-1}
RainFall	Diag.	4	486.9	479.3	505.9	507.9	504.4	503.4	492.6	502.9	505.3	495.1	505.5	**462.2**	486.2	497.3
	No diag.	1	430.1	436.5	446.4	444.1	453.5	441.1	426.1	440.3	449.5	445.1	455.2	**403.3**	432.9	444.1
River Run-off	Diag.	4	508.1	**500.6**	511.3	515.3	503.8	513.7	620.9	1188.6	504.9	515.8	503.9	503.9	500.2	517.0
	No diag.	1	458.7	446.3	454.4	450.4	**438.1**	458.5	446.6	446.8	451.7	450.4	**438.0**	446.3	446.1	450.5
SST	Diag.	4	504.6	507.9	**491.7**	512.5	513.5	509.3	513.5	512.7	502.5	512.0	498.4	506.2	512.6	504.1
	No diag.	1	447.1	454.1	443.9	457.5	458.6	445.4	453.0	457.7	451.1	452.1	454.2	454.7	454.0	**438.4**
Ekman	Diag.	4	505.5	708.6	496.7	510.6	500.0	496.7	**480.4**	512.4	863.6	662.4	745.5	750.2	696.0	904.1
	No diag.	1	457.3	448.5	453.0	452.1	436.5	449.6	**432.5**	450.9	448.7	448.6	448.7	448.6	448.5	448.7
WS_u	Diag.	4	510.2	515.4	504.5	509.8	507.7	508.7	500.8	507.3	500.1	501.1	505.0	499.9	**495.4**	500.6
	No diag.	1	448.2	460.9	448.5	445.5	439.4	449.0	436.0	447.7	449.8	445.6	447.4	442.0	**435.1**	441.6
WS_v	Diag.	4	514.9	504.8	500.0	517.8	494.4	506.0	492.7	519.7	**481.7**	503.7	510.4	500.9	485.9	504.9
	No diag.	1	462.0	442.5	450.3	464.3	464.3	454.1	444.2	466.8	451.9	453.0	455.6	441.7	**436.6**	446.1
$GeoCURR_m$	Diag.	4	821.5	761.3	979.8	800.8	989.8	775.1	764.8	599.0	800.8	800.9	800.8	800.7	800.7	800.9
	No diag.	1	459.1	445.1	445.0	445.1	452.9	456.0	459.1	445.1	439.3	**438.7**	**438.7**	445.1	445.0	438.8
$GeoCURR_z$	Diag.	4	1005.0	800.7	800.7	800.7	1422.1	900.4	1057.3	800.9	800.9	930.1	800.7	1245.3	795.4	800.9
	No diag.	1	459.2	445.1	445.0	445.1	453.0	456.0	459.1	445.1	**438.8**	439.6	**438.8**	445.0	445.0	**438.8**
WeMOi	Diag.	4	502.4	501.6	497.9	493.0	506.1	511.7	509.8	499.8	501.9	501.0	518.1	489.6	487.1	510.1
	No diag.	1	442.1	450.6	442.8	431.8	456.3	452.1	452.6	442.9	442.2	438.9	464.6	437.2	**429.1**	455.0

Bold values represent the lower AIC for each variable combination.

Table 7. AIC values for the third set of DFA models with explanatory variables combination (just for one trend symmetric non-diagonal matrix).

ID	Combination	AIC	ID	Combination	AIC
1	rai_Raint^{-1} + rai_WeMOit^{-1}	367.15	27	rai_WS$_v t^{-1}$ + sum_Rivert^{-1}	423.18
2	rai_Raint^{-1} + rai_Ekman	375.80	28	rai_WS$_v^{-1}$+ W_SST	417.97
3	rai_Raint^{-1} + rai_WS$_u^{-1}$	388.80	29	rai_WS$_v^{-1}$ + sum_GC$_m^{-1}$	423.15
4	rai_Rain^{-1} + rai_WS$_v^{-1}$	409.53	30	rai_WS$_v^{-1}$ + sum_GC$_z^{-1}$	423.08
5	rai_Rain^{-1} + sum_River^{-1}	393.16	31	sum_River^{-1} + W_SST	418.25
6	rai_Rain^{-1} + W_SST	390.03	32	sum_River^{-1} + sum_GC$_m^{-1}$	423.77
7	rai_Rain^{-1} + sum_GC$_m^{-1}$	392.25	33	sum_River^{-1} + sum_GC$_z^{-1}$	423.75
8	rai_Rain^{-1} + sum_GC$_z^{-1}$	393.00	34	spr_SST^{-1} + sum_GC$_m^{-1}$	421.78
9	rai_WeMOi^{-1} + rai_Ekman	404.48	35	spr_SST^{-1} + sum_GC$_z^{-1}$	422.03
10	rai_WeMOi^{-1} + rai_WS$_u^{-1}$	415.89	36	sum_GC$_m^{-1}$ + sum_GC$_z^{-1}$	430.17
11	rai_WeMOi^{-1} + rai_WS$_v^{-1}$	417.27	37	rai_Rain^{-1} + rai_WeMOi^{-1} + rai_Ws$_v^{-1}$	373.53
12	rai_WeMOi^{-1} + sum_River^{-1}	409.63	38	rai_Rain^{-1} + rai_WeMOi^{-1} + rai_Ekman	340.47
13	rai_WeMOi^{-1} + W_SST	408.98	39	rai_Rain^{-1} + rai_WeMOi^{-1} + rai_WS$_u^{-1}$	355.36
14	rai_WeMOi^{-1} + sum_GC$_m^{-1}$	422.01	40	rai_Rain^{-1} + rai_WeMOi^{-1} + sum_River^{-1}	334.57
15	rai_WeMOi^{-1} + sum_GC$_z^{-1}$	422.20	41	rai_Rain^{-1} + rai_WeMOi^{-1} + W_SST	348.61
16	rai_Ekman + rai_WS$_u^{-1}$	414.48	42	rai_Rain^{-1} + rai_Ekman + rai_WS$_v^{-1}$	375.54
17	rai_Ekman + rai_WS$_v^{-1}$	411.30	43	rai_Rain^{-1} + rai_Ekman + rai_WS$_u^{-1}$	354.55
18	rai_Ekman + sum_River^{-1}	421.75	44	rai_Rain^{-1} + rai_Ekman + sum_River^{-1}	367.01
19	rai_Ekman + W_SST	417.93	45	rai_Rain^{-1} + rai_Ekman + W_SST	359.73
20	rai_Ekman + sum_GC$_m^{-1}$	424.28	46	rai_Rain^{-1} + rai_WS$_v^{-1}$ + rai_WS$_u^{-1}$	381.65
21	rai_Ekman + sum_GC$_z^{-1}$	424.29	47	rai_Rain^{-1} + rai_WS$_v^{-1}$ + sum_River^{-1}	396.35
22	rai_WS$_u^{-1}$ + rai_WS$_v^{-1}$	411.22	48	rai_Rain^{-1} + rai_WS$_v^{-1}$ + W_SST	387.34
23	rai_WS$_u^{-1}$ + sum_River^{-1}	430.40	49	rai_Rain^{-1} + rai_WS$_u^{-1}$ + sum_River^{-1}	377.97
24	rai_WS$_u^{-1}$ + W_SST	428.70	50	rai_Rain^{-1} + rai_WS$_u^{-1}$ + W_SST	375.42
25	rai_WS$_u^{-1}$ + sum_GC$_m^{-1}$	460.40	51	rai_Rain^{-1} + sum_River^{-1} + W_SST	370.27
26	rai_WS$_u^{-1}$ + sum_GC$_z^{-1}$	445.22			

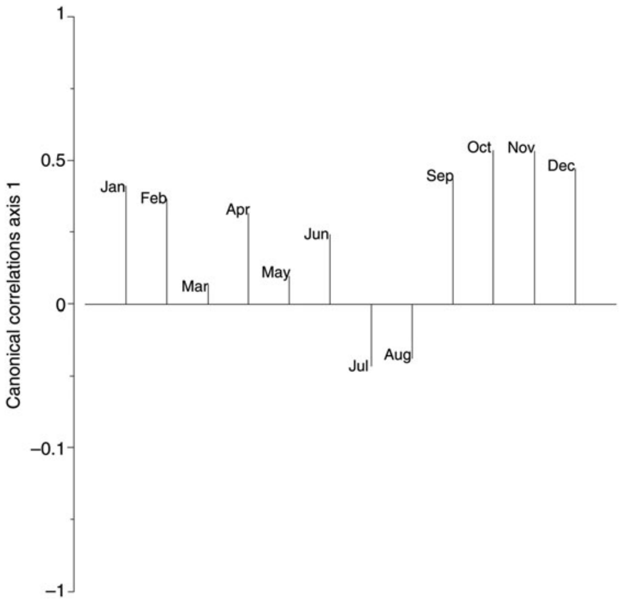

Figure 5. Canonical correlations for the DFA model no. 40 (third set). Correlations > -0.5 or >0.5 are significant ($p < 0.05$).

Other than rainfall, strong negative correlations were also found between LPUE and summer river run-off lagged 1 year, especially for spring and summer. Erzini (2005) also found that the most important variable affecting trends of 12 landings time-series of important fisheries resources in the same area was the Guadiana river run-off. Sea surface temperature (dry season average: April–September) lagged 1 year was also significantly negatively correlated with LPUE, especially for spring and early summer. A similar pattern was reported by Chédia *et al.* (2010) in the Mediterranean (Tunisia) who found a negative correlation between SST and cpue of *O. vulgaris* with a 4–6-month lag, corresponding to the preceding paralarval period. Our results suggest that warmer waters during spring, especially in April, seem to be detrimental to the LPUE of the next year, especially for the recruitment months. Another variable which presented lower AIC was the horizontal component of windstress lagged 1 year (rainy season average). In Galicia, González (2005) found that windstress structure during spring–summer (before the hatching peak) and autumn–winter (during the planktonic stage) explained up to 85% of the total variance of the adult catch. Moreover, Otero *et al.* (2008) in the same area proposed that *O. vulgaris* spawning is synchronized with upwelling-relaxation events, with a single peak in spring.

Recently, Roura (2013) proposed an oceanic life cycle for *O. vulgaris* during its planktonic phase in upwelling areas (Ria de Vigo, northwest Spain), presenting evidence that *O. vulgaris* paralarvae are washed offshore during upwelling events, despite the coastal distribution of juveniles and adults. Weighing the latter facts, and considering that Algarve fishing grounds display different hydrodynamic and meteorological conditions, there may be a different early life-history strategy in the south of Portugal. However, the upwelling-relaxation coupling system in South Portugal which extends to leeward Algarve plays an important role in the cephalopod plankton community in the area (Moreno *et al.*, 2008), with some similarities with Ria the Vigo.

In any attempt to evaluate the underlying relationships between octopus reproductive biology, recruitment, and fishery dynamics,

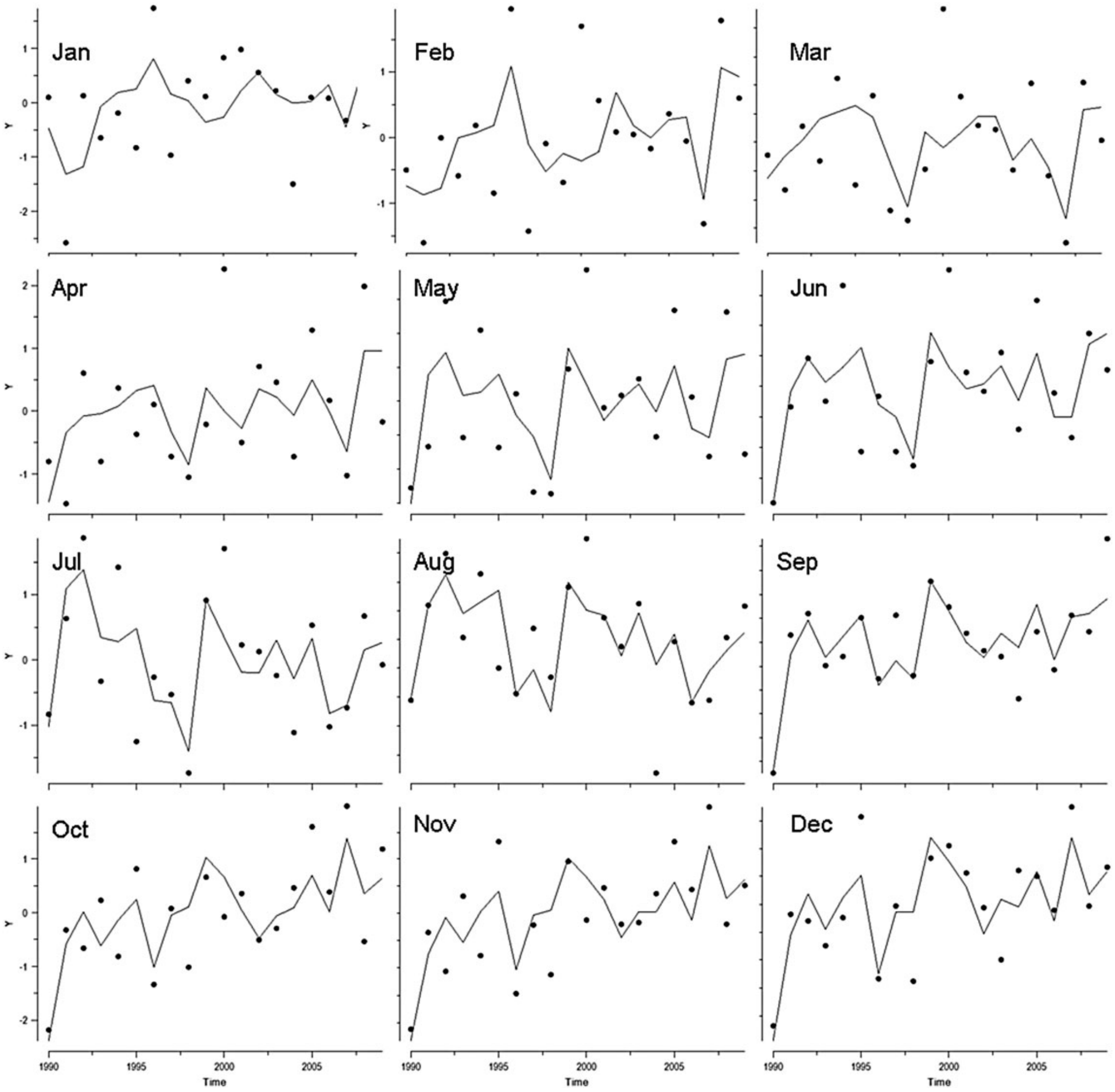

Figure 6. Observed (filled circles) and fitted (lines) LPUE series from the DFA model no. 40 with one common trend and three explanatory variables (rainy season value of RainFall^{-1}, WeMOi^{-1}, and summer river run-off $^{-1}$) and a positive non-diagonal matrix. *y*-axis is standardized. Months are represented by initials (JAN = January, FEB = February, etc.) and refer to LPUE time-series.

interpretations based on LPUE–environment interactions should be considered with care. Knowledge of the most relevant processes, both oceanographic and biological, is essential. The effects of rainfall and the other environmental variables analysed on *O. vulgaris* LPUE should not only be considered during the sensitive planktonic cycle, but also at important stages, such as mating and spawning. In terms of fisheries biology, the octopus life cycle in the region is still not entirely clear, with detailed information on reproductive timing still lacking. There is also a need for information on age and growth to back-calculate age and identify specific cohorts, thereby contributing to a better understanding of octopus dynamics in relation to fishing and environmental variability. Notwithstanding, the results of this study have shed light on the octopus population and fishery dynamics at the regional scale, identifying the most important environmental variables influencing recruitment, and helping to explain the observed patterns in LPUE.

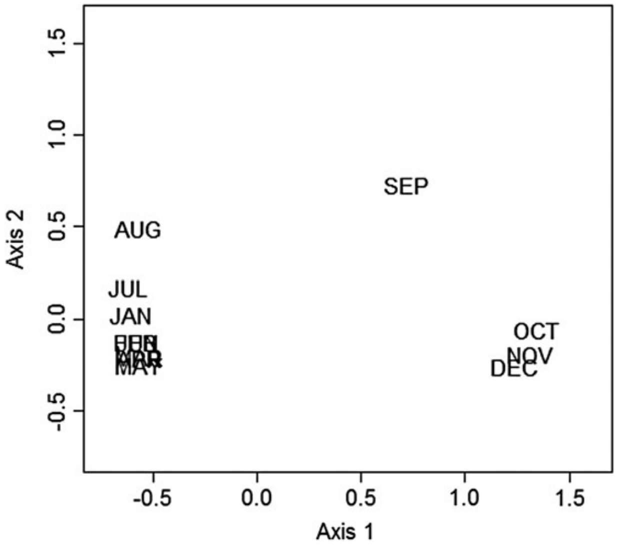

Figure 7. MDS applied on the error covariance matrix from model no. 40. Months are represented by initials (JAN = January, FEB = February, etc.) and refer to LPUE time-series.

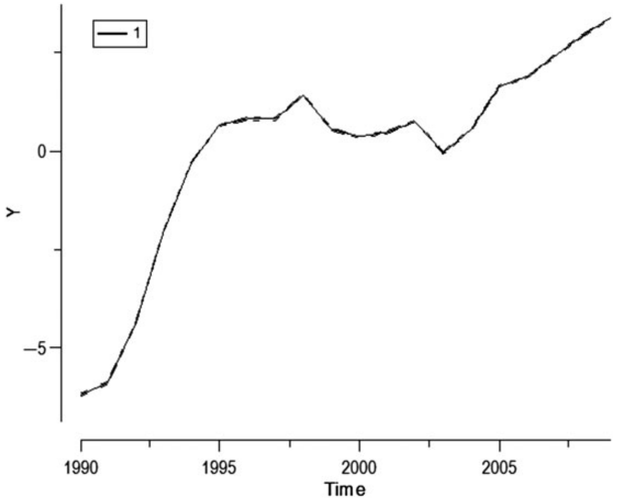

Figure 8. The estimated common trend for model no. 40 (standardized). Dashed lines represent 95% confident intervals.

Acknowledgements

I would like to thank Dr. Francisco Leitão (Xico) for the support with the data analyses. Telma Conduto for her company in the office and sharing knowledge. Data used in this analyses was provided by Dra. Paula Cristina Ramalho of the Fisheries and Aquaculture Directorate General (DGPA). The present work is the result of a PhD scholarship awarded to the first author by the Portuguese Science Foundation (reference SFRH/BD/51274/2010) as part of the Portuguese-Venezuelan agreement on higher education.

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Handling editor: Rochelle Seitz

ICES Journal of Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2242–2251. doi:10.1093/icesjms/fst220

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

Are the Laurentian Great Lakes great enough for Hjort?

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Janssen, J., Marsden, J. E., Hrabik, T. R., and Stockwell, J. D. Are the Laurentian Great Lakes great enough for Hjort? – ICES Journal of Marine Science, 71: 2242–2251.

Received 1 July 2013; accepted 19 November 2013; advance access publication 15 January 2014.

Hjort's insights on marine fish recruitment and larval fish advection are presumed not applicable to freshwater lakes because most freshwater lakes are small. The Laurentian Great Lakes (LGL), however, are large enough for certain oceanic-type hydrodynamics, such as strong currents and upwelling, to affect the distribution and survival of larval fish and thus fall under Hjort's purview. However, there are evolutionary constraints because LGL species underwent an evolutionary bottleneck during glaciation, ~10 000 years BP. We consider three narratives pertinent to both the spatial scale and the evolutionary time-scale of the LGL. The first reviews recent evidence of offshore advection and subsequent cross-lake dispersal of larval and juvenile yellow perch, a coastal demersal species in Lake Michigan. The second narrative suggests that biotic interactions, rather than spatial scale itself, could account for the transition in the critical period of Lake Michigan yellow perch period from a juvenile to a larval critical period. In the third narrative, we consider whether the deep LGL lack a significant native pelagic larval fish predator. We propose that the LGL, in combination with the older World's Great Lakes, present an opportunity to explore evolution and adaptation of fish to oceanic type physical conditions.

Keywords: larval fish, Laurentian Great Lakes, vertical migration.

Introduction

Population biology has diverse roots commonly associated with different taxa and habitats, and often generating divergent hypotheses and methodologies. To generate more robust hypotheses and methodologies, these roots must intersect and anastomose. We propose that, because the average early life histories of freshwater vs. marine fish tend to be different (Houde, 1994), no truly robust understanding of fish population biology as it relates to evolutionary pressures have yet emerged. The driving evolutionary pressures for freshwater vs. marine species are more likely to be due to scale, rather than salinity. Hence, the study of early life histories across size scales could illuminate the role of scale in early life-history evolution. Because freshwater systems vary greatly in both size and age, we propose that they are natural laboratories for the study of early life-history evolution of fish, with the potential to create a broader context for the seminal works of Hjort (1914, 1926).

Hjort (1914, 1926) introduced the highly influential concepts of "critical period" for larval marine fish survival, and "aberrant drift" of larvae advected to variably viable locations. Cushing (1975, 1990) creatively combined these concepts with his match–mismatch hypothesis, which became technologically testable at waterscape scale via innovations in satellite imagery (Platt and Csar Fuentes-Yaco, 2003). Houde (2008) provided robust analysis of post-Hjort developments that offers an excellent framework for further progress for research on variability in marine fish recruitment.

Are any of these advances in marine fish population biology applicable to freshwater fish? Houde (1994) argued that the early life histories of average freshwater fish were very different from typical marine species in that freshwater fish larvae tended to be both larger and have a short or no pelagic period on which advection could act. While Houde (1994) showed clearly that freshwater larval fish average larger than marine larval fish and have a shorter average pelagic period, there was variation and overlap. We expect that lessons in evolutionary pressures driving these differences can be derived from the extremes in the variation. Rather than re-analyse Houde's (1994) more than adequate work, we note that the chief freshwater species that we discuss, the yellow perch (*Perca flavescens*), tends to have larvae of size similar to those of the Atlantic herring (*Clupea harengus*), the chief species considered by Hjort (1914). Reported sizes for yellow perch larvae are 5–8 mm TL at swim-up (Auer, 1982) and 4–9 mm for Atlantic herring (Reid *et al.*, 1999).

The scale of most lakes (from now on "common lakes ", lakes smaller than ~50–100 km^2) would preclude much larval drift or the impact of drift. An extended pelagic larval stage, typical of marine fish, renders them more susceptible to predation and starvation and the interaction of the two. Hence, for marine fish, recruitment would likely be most strongly related to the survival of larvae. For freshwater fish, Houde (1994) argued that survival of the juvenile stage, rather than the larval stage, was more likely to correlate with recruitment, in large part because the pelagic period was short or non-existent. An unfortunate consequence of Houde's (1994) conclusions was that marine and freshwater biologists could conveniently ignore each other's work.

We propose that the dichotomy between marine vs. freshwater fish early life history and consequent fisheries ecology is artificial and should be replaced by a continuum approach. There are at least two relevant scales, a size scale and an evolutionary scale, which cover many orders of magnitude (Figure 1). We propose that spatial scale is a selective factor in fish early life history. System sizes range from ponds on the scale of hectares to the three largest oceans, with common lakes, large lakes, and the World's Great Lakes (WGL) in between. The evolutionary time-scale ranges from northern hemisphere glacial lakes (~10^4 years) to oceans (~10^8 years). The oceans are much older, so we have taken their relevant age as approximating the radiation of the teleosts, given as ~1.5 × 10^8 years based on fossils or possibly twice that based on DNA (Hurley *et al.*, 2007). The source of founding populations for fish in ponds and lakes is usually rivers, which generally have a longer life (assuming rivers originate mainly with tectonic uplift, ~2–3 × 10^8 years for eastern North America), or marine environments.

For the evolutionary time-scale, intermediate times are well studied for certain oceanic islands. The classic example is the Galapagos (Darwin's) finches, thought to have begun their radiation a few million years ago, comparable with Lake Baikal and the African Great Lakes (Grant and Grant, 1986). The Laurentian Great Lakes (LGL) have existed long enough for some intrageneric speciation (Todd *et al.*, 1981) and microevolution (Crowder, 1986). At an intermediate evolutionary time-scale, the older WGL have had speciation at the generic level (African Cichlidae, see Fryer 1972) and even family level (Lake Baikal's Cottoidea, see Sideleva 2003).

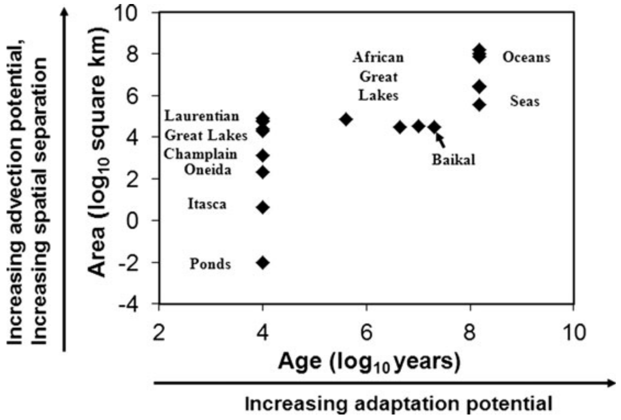

Figure 1. Bodies of water, from ponds to oceans arranged by evolutionary time and surface area scales. The time-scale is approximate and taken as about the time of glacial retreat for the LGL and smaller North American and European lakes (Hubbs *et al.*, 2004). The evolutionary ages of the older World's Great Lakes is approximately million of years, but still debated. For oceans and seas (Baltic and Mediterranean shown but not labelled), we take the evolutionary time as approximating the radiation of teleosts, estimated to be 150–300 million years (Hurley *et al.*, 2007).

We propose that a linkage between recruitment dynamic principles between small bodies of water, i.e. common lakes, and the much larger marine systems, lies in comparisons with the intermediate scale, the WGL. We mainly focus on the four deep LGL (lakes Superior, Michigan, Huron, and Ontario, maximum depth ranges from ~250 to 400 m, from now on "LGL-DEEP") because they share a similar founding fish fauna, coregonines and sculpins, with the intermediate age Lake Baikal (Kozhova and Izmest'iva, 1998). These LGL-DEEP share with Lake Baikal, seas, and oceans a relatively small littoral zone area. We initially discuss the yellow perch (*P. flavescens*), because it has a pelagic larval phase across a gradient of lake sizes and it undergoes a transition to becoming demersal in its first summer. The other native LGL-DEEP fish with pelagic larvae are mostly either pelagic or bentho-pelagic as adults (ciscoes, *Coregonus* spp.), and so do not undergo a demersal transition, or have marine relatives. The species with marine relatives include deepwater sculpin, *Myoxocephalus* (=*Triglopsis*) *thompsoni*, which was once considered to be conspecific with the marine fourhorned sculpin (*Myoxocephalus quadricornis*) and the burbot, *Lota lota* which is the only freshwater gadid (Hubbs *et al.*, 2004). The question we address is "are the LGL large enough and old enough that Hjort's larval stage 'critical period' and/or 'adverse advection' are pertinent to fish population biology in freshwater systems?" We provide three narratives for consideration, beginning with a demonstration of advection, upon which discussion of a critical period depends. The critical period for yellow perch may have been imposed by the invasive marine coastal alewife (*Alosa pseudoharengus*) so our final narrative concerns whether the LGL-DEEP lack significant predation on pelagic larvae.

Narrative 1: the spatial scale at which larval fish advection is important

Being terrestrial, humans inherently orient to terrestrial features that usually change little in a lifetime. This "geoscape" extends under the water as a "benthoscape" that is typically poorly mapped and too often ignored (Caddy, 2014). Hjort (1914) presented compelling evidence that fisheries ecologists must also study the water masses that form a "hydroscape" that is much more dynamic than the benthoscape. Those benthic and bentho-pelagic fish with a pelagic larval phase have a challenging transition from the hydroscape to the benthoscape because the hydroscape may advect them to an inappropriate benthoscape. A clear example in the LGL-DEEP is the occasional drift of deepwater sculpin larvae, spawned in depths greater than 70 m in Lake Huron, to 9 m depth in the west end of Lake Erie. Larvae drift ~130 km, transiting through two channels (St Clair River and Detroit River) and an intermediate shallow lake (Lake St Clair; Roseman *et al.*, 1998). Lake Erie does not sustain a deepwater sculpin population.

Narrative 1 focuses on yellow perch, a common piscivore in North American ponds, lakes, and slow rivers. Yellow perch are present in the bays of each of the LGL-DEEP and in the three basins of Lake Erie, where the populations are mostly associated with major tributaries and associated bays (Sepulveda-Villet *et al.*, 2009); Lake Michigan is the only LGL-DEEP that supports a main basin yellow perch population. Their change to adult habitat is associated with a change in morphological ontogeny: yellow perch generally acquire the colour pattern of the adult at ~25 mm, the size at which they typically become littoral zone fish, whereas in Lake Michigan they typically remain pelagic with their littoral zone colouration until they are ~50 mm (Dettmers *et al.*, 2005; Weber *et al.*, 2011).

The early life history of Lake Michigan yellow perch is similar to many marine species because it has a long pelagic period before it becomes demersal (Dettmers *et al.*, 2005). The eggs, however, are demersal and are protected in a noxious gelatinous sheath. In common lakes, the eggs are spawned over vegetation and submerged woody debris, but in Lake Michigan yellow perch spawn in rocky habitat (Robillard and Marsden, 2001), primarily found along the western (Illinois and Wisconsin) shoreline; some spawning does occur at a few rocky sites along the eastern (Michigan) shore. There are no documented spawning sites along the sandy southern shore (B. Briedert, Indiana Department of Natural Resources, Indiana, pers. comm.).

Recent research has begun to describe advection processes in Lake Michigan yellow perch (Beletsky *et al.*, 2004, 2007; Dettmers *et al.*, 2005). Before these studies, many assumed that yellow perch larvae recruited near spawning sites. The incentive for testing this assumption emerged during the 1990s when the Lake Michigan yellow perch population exhibited sufficiently poor recruitment to close the commercial fishery and restrict the sport fishery (Francis *et al.*, 1996). Early larval stages were abundant in the nearshore zone, but feeding larvae and small juveniles were scarce (Marsden and Robillard, 2004). Over several years, larval assessments expanded from coastal and regional efforts to cross-lake sampling with larger/older individuals found offshore (Dettmers *et al.*, 2005). Sampling at multiple scales, based in part on hydrodynamic conditions, revealed that yellow perch larvae were advected from coastal spawning areas to the pelagia (Dettmers *et al.*, 2005). Passive hydrodynamic processes were sufficient to explain advection, including subsequent return of juveniles to the coast (Beletsky *et al.*, 2007). Early larvae were advected offshore during upwelling events but could reappear near shore during downwelling events (Dettmers *et al.*, 2005). Once advected offshore, the larvae are subjected to the complexities of offshore currents (Mortimer, 2004) so predicted drift varies among years (Beletsky *et al.*, 2004, 2007).

The relevant hydrodynamics driving larval yellow perch advection relates to spring warming of Lake Michigan (and the three other LGL-DEEP) and are different from those of Lake Erie, small lakes, or coastal marine waters. Lake Michigan completes thermal stratification in late May/early June, about the time that yellow perch hatch. Stratification first involves the development of a narrow coastal "thermal bar" of water warmer than 4°C while the centre is cooler than 4°C. Offshore warming in this case proceeds by a combination of solar warming and buoyant spreading of the warmer water from the coasts to the middle (Mortimer, 2004). Beletsky *et al.*'s (2004, 2007) models of passive yellow perch advection show that passive particles have a general drift offshore augmented by the pulses of more rapid offshore drift driven by upwelling events. The hydrodynamic model also predicted significant between-year variation in average current (Figure 2) and, although the modelling and corresponding sampling time-series was only 6 years, demersal yellow perch distribution was close to that predicted by the modelling (Beletsky *et al.*, 2007).

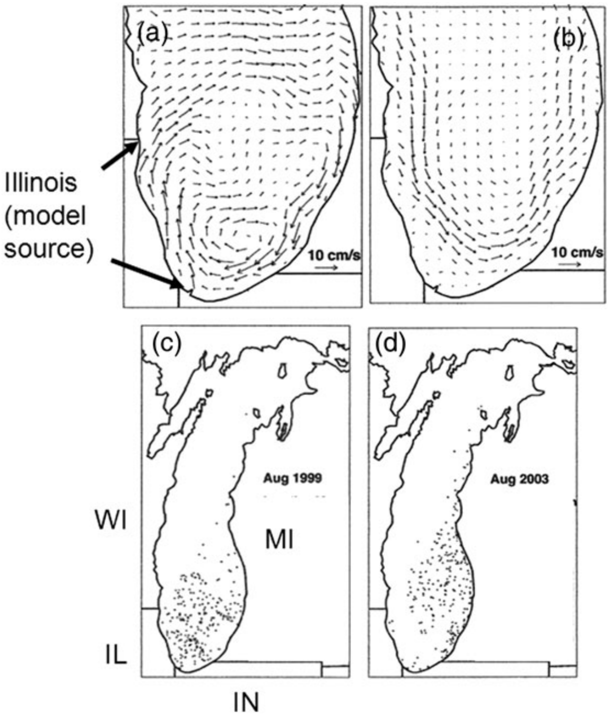

Figure 2. Larval yellow perch drift model results (Beletsky *et al.*, 2007) showing the two most extreme years, 1999 and 2003, from models runs from 1998 to 2003. States are, from west side, WI, Wisconsin; IL, Illinois; IN, Indiana; MI, Michigan. The model includes a temperature-based larval growth model. Always, the model larval is passive drifters originating from Illinois only (arrows). In 1999, the average drift in the southern basin was clockwise in a tight gyre, and in 2003, it was anticlockwise in a more open gyre. Consequently, the modelled drift showed greater dispersion of larvae (here at >30 mm in August) in 2003 than in 1999. Further modelling results in Beletsky *et al.* (2007) predict settlement at 50 mm that corresponded to relative abundance of fish caught in surveys.

Parallel to Hjort's (1914) use of Atlantic herring annulus growth pattern "signatures" to demonstrate mixing of fish from differing geographic origins, daily growth rings of Lake Michigan yellow perch larvae indicate significant offshore mixing of larvae of differing ages (Weber *et al.*, 2011). Larvae that hatch at different times and originated from different spawning grounds become mixed during the pelagic phase. The hydrodynamic mixing likely drives genetic mixing. Southern basin yellow perch are genetically homogenous but are genetically distinguishable from the population in Lake Michigan's largest bay, Green Bay, as well as coastal connecting lakes (Miller, 2003), which each contain yellow perch populations that spawn about a month earlier than the main basin population, presumably because they warm earlier.

The location where a yellow perch becomes demersal likely makes a difference for juvenile growth, so there can be "adverse advection". Janssen and Luebke (2004) showed that newly demersal yellow perch preferred rocky habitat and Horns (2001) showed that post-juveniles grew faster along the rocky west coast compared with the sandy southern and east coasts, despite the latter being warmer. In common lakes, hydrodynamic processes are less important than the swimming ability of larval fish. The range of size of lakes that harbour *Perca* spp. covers many orders of magnitude, from Lake Michigan to ponds of only a few hectares. Hutchinson's (1957) review of common lakes indicates maximum currents are only a few cm s^{-1}, similar to the swimming speed of early fish larvae (Houde, 1969).

At what lake size are currents sufficient to override a larval yellow perch's swimming ability? Leis (2006) posed related questions regarding the relative importance of hydrodynamics and swimming and discussed diverse tactics by which larval fish can use hydrodynamics to their advantage. Transition from passive drift in yellow perch likely occurs earlier in Oneida Lake (New York state, 20 670 ha) compared with Lake Michigan. Oneida Lake currents typically range between 4 and 10 cm s^{-1}, which exceed Houde's (1969) laboratory-estimated swimming speed for yellow perch up to 9.5 mm in length. Lake Michigan currents are typically between ∼10 and 15 cm s^{-1} but episodically can be much greater (Beletsky and Schwab, 2001; Mortimer, 2004; Beletsky *et al.*, 2007). Coastal currents commonly are closer to 1 m s^{-1} (unpublished buoy data). Because there is a continuum in the strength of hydrodynamic effects from similar to less than the swimming speed of newly hatched yellow perch to the large currents of the LGL-DEEP, we hypothesize the importance of advection should increase approximately with lake size (Figure 1).

The pelagic period and size at which *Perca* becomes benthic is less for lakes smaller than Lake Michigan and apparently increase with lake size (Urho, 1996). The minimum Urho reported was ∼2 weeks for a 13-ha pond in Finland. Those *Perca* left the limnetic (pelagic) zone at a length of ∼12 mm. In Crystal Lake, WI (26 ha), a lake with negligible currents, Hrabik *et al.* (2001) found that yellow perch began to arrive in the littoral zone at ∼14 mm. Fish at intermediate lengths became littoral in intermediate-sized lakes (Urho, 1996). In a larger lake (Lake Itasca, MN, USA, 4360 ha), Whiteside *et al.* (1985) reported that fish became littoral at ∼23 mm, a length at which they begin to take on the vertical striped colouration of the littoral zone juveniles and adults. Whiteside *et al.*'s (1985) fish were pelagic for an estimated 45 d. Urho (1996) reported that at Lake Constance (Switzerland, 57 000 ha) *Perca fluviatilis* became littoral at 30–40 mm.

We suspect that Lake Michigan *Perca* have the longest pelagic period of any population of *Perca*. The likely pelagic period for Lake Michigan yellow perch is 60 or more days (Weber *et al.*, 2011) with hatching occurring in late May to early June and juveniles becoming demersal in early August to as late as mid-September (Beletsky *et al.*, 2007; Weber *et al.*, 2011). Anecdotally, we have collected pelagic, 60–70 mm TL, yellow perch in mid-September, 60 km from the nearest shore. Yellow perch captured nearshore at that time, in a few meters of water are of similar TL. Fish as small as 28 mm TL are occasionally found in shallow water earlier (Weber *et al.*, 2011); these are about the length that yellow perch become demersal in smaller lakes (Urho, 1996) so it may be that yellow perch are still passive drifters (pseudolarvae) rather than actively staying offshore. Whether yellow perch that are still offshore in mid-September ever encounter coastal waters or are lost (adverse advection at its most dangerous) is unknown.

The long pelagic period for Lake Michigan yellow perch appears to be imposed by circumstance rather than evolution. Assuming a post-metamorphic juvenile yellow perch of ∼20–25 mm has a morphology, including the vertical striped pattern of all larger stages, adapted to beginning a demersal existence, those Lake Michigan yellow perch that are still pelagic at (say) 50 mm have an inappropriate morphotype for a pelagic existence. The colour pattern of vertical bars is very dissimilar from the silvery counter-shaded pattern of most pelagic fish and could render them relatively vulnerable to offshore predation. However, in the absence of predation, the pelagic residence could offer access to vertically moving plankton.

Can yellow perch survive adverse advection? We believe the answer is yes, because most of the preferred rocky habitat for both feeding and spawning is along the west coast of Lake Michigan and currents tend to take the larvae towards the east coast. But there is less risk to being pelagic as a larva than for most marine fish. Beletsky *et al.*'s (2007) hydrodynamic model assumes no active swimming towards a coast. Under that assumption, many yellow perch do reach shallow water, but many do not. For marine fish, there are multiple active mechanisms to avoid adverse advection (Leis, 2006). Oriented swimming to a coast is possible if there are sufficient cues for orientation such has been indicated for several marine demersal fish with pelagic larvae (Atema *et al.*, 2002; Wright *et al.*, 2005). Other means of actively avoiding dispersal include vertical migrations between differentially moving deep and shallow currents to remain close to demersal habitat (Paris and Cowen, 2004). For now, the issue of whether yellow perch pelagic juveniles are totally passive or actively seek the littoral zone remains unresolved. But, resolving that question would be a clue to whether attaining demersal nursery habitat is an evolutionary challenge.

Narrative 2: the yellow perch "critical period" and spatial scale

Whereas Hjort (1914) focused on the role of first feeding on critical periods, subsequent work (e.g. Folkvord and Hunter 1986; Rice *et al.* 1987) include predation because slow-growing or nutritionally weakened larvae are more vulnerable to predation. Houde (1994) argued that the critical period that establishes year-class strength is more likely to be determined in the larval phase for marine fish and the juvenile phase for freshwater species because a pelagic larval phase was generally short or absent in freshwater fish. Because spatial scale influences the pelagic duration of *Perca*, we have an opportunity to test this hypothesis for a single species across a gradient of lake sizes. Scale, not species, becomes the primary factor, and evolution is held at the post-glaciation timescale for common lakes, intermediate lakes, and LGL.

Based on lake size and Houde's (1994) characterizations for marine vs. freshwater species, Lake Michigan yellow perch recruitment should be more similar to that for marine species, while in smaller bodies of water it should be more typical of freshwater species. Nielsen (1980) argued that *Perca* year-class strength is generally determined in their first year. In Lake Michigan, however, the critical period occurs before settlement, based on evidence of low overwinter, post-settlement, mortality (Fitzgerald *et al.*, 2004). The emerging evidence is that recruitment is now established during the pelagic stage by an invasive obligate planktivorous clupeid, alewife (*A. pseudoharengus*, originally detected in 1949 and abundant by the 1960s). Shroyer and McComish (2000) found a negative correlation between alewife (age 2+) and yellow perch year-class strength (Figure 3a). Note that the range of yellow perch recruitment ranges over almost 3 orders of magnitude, a fluctuation comparable with that reported for Atlantic herring by Hjort (1914). Corroborating evidence of an alewife impact was presented by Redman *et al.* (2011); their most parsimonious of several multiple regression models indicated negative impacts by alewife and/or low zooplankton abundance.

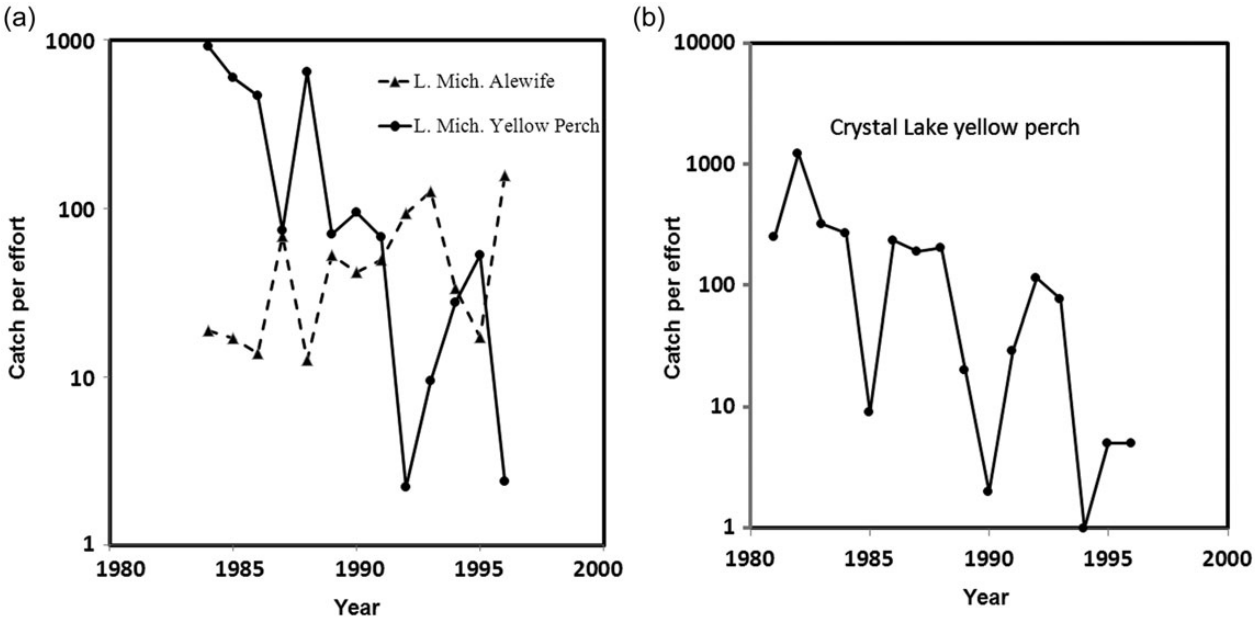

Figure 3. Recruitment dynamics for age-0 yellow perch and alewife in southern Lake Michigan and yellow perch in Crystal Lake, Wisconsin, USA. (a) For Lake Michigan, recruitment of yellow perch is negatively correlated with alewife abundance ($r^2 = 0.736$ for $\log_e$ transformed catch per effort for both species, Shroyer and McComish, 2000). This suggests that in Lake Michigan yellow perch recruitment is decoupled from its own population and indirectly coupled to factors that impact alewife abundance. Data based on bottom trawls, see Shroyer and McComish (2000) for details. (b) In Crystal Lake, there is a cycle consistent with modelling a population that self-regulates by cannibalism (Sanderson *et al.*, 1999). See Sanderson *et al.* for collection details.

The mechanism by which alewife might impact yellow perch recruitment could be via prey availability or predation on larval yellow perch. High alewife densities shift zooplankton size distributions to smaller sizes both for small lakes (Brooks and Dodson, 1965) as well as Lake Michigan (Wells, 1970; Evans and Jude, 1986) so the mechanism of impact could be slow/growth with consequent higher predation mortality or even starvation. The mechanism could also be alewife predation on yellow perch larvae which has been demonstrated in Lake Ontario bays (Brandt *et al.*, 1987; Mason and Brandt, 1996).

Some indication that primary production and consequent zooplankton prey availability affects pelagic yellow perch survival derives from an episodic event that correlates with relatively good recruitment for both yellow perch and alewife of the same year class. A good year class for both species was 1998 and, just before hatching for both species, a 160-kph wind event destratified Lake Michigan. Pelagic primary production is greatly diminished once the lake is stratified and this wind event increased primary production over a typical year by an estimated 25% (Figure 4, based on Lesht *et al.*, 2002). Note in Figure 4 that the phytoplankton concentrations are very patchy. The pixel size for the sampling grid is 1 km^2 (100 ha), larger than the size of smallest *Perca* lakes discussed in the advection narrative. Hjort (1914) noted that good year classes could be synchronized among several species, noting the good year classes of 1904 for Atlantic herring, Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*). What might have driven this 1904 synchrony is unknown.

For smaller bodies of water, there are several studies that indicate that predation on juvenile yellow perch, including cannibalism, rather than on larvae, determines year-class strength. One of the more interesting studies of yellow perch recruitment was the demonstration of cyclic recruitment in 26 ha Crystal Lake (WI) driven by cannibalism on age-0 juveniles (Sanderson *et al.*, 1999). When older yellow perch are abundant they impede recruitment via cannibalism and competition, with senescence of older perch there is a burst of recruitment (Figure 3b). Similarly, the suppression of recruitment by a prior strong year class was demonstrated for yellow perch in Lake Michigan in 1987–1997 (Marsden and Robillard, 2004). In contrast, Shroyer and McComish (2000) showed that yellow perch abundance in southern Lake Michigan for a similar period fluctuated inversely with abundance of alewife (Figure 3a). Assuming that yellow perch recruitment in southern Lake Michigan, is driven by alewife impact on the larval stage, then yellow perch recruitment is related to alewife recruitment.

Perhaps a reverse, in terms of spatial scale, and artificial, situation of cannibalism exerting population control exists in Atlantic cod mariculture. In such ponds, the Atlantic cod may consume their own offspring with negative consequences (Folkvord and Otterå, 1993). Under this small scale, which lacks an obligate planktivore to prey on larval stages, the Atlantic cod appear similar to Sanderson *et al.*'s (1999) cannibalistic yellow perch.

Other predators in lakes, such as walleye, are also associated with the littoral zone and can have a negative impact on yellow perch recruitment (Nielsen, 1980; Rudstam *et al.*, 1996). In general *Perca* becomes piscivorous at ~15 cm TL while walleye become piscivorous at the end of their first summer, at lengths of ~5 cm or less.

The likelihood that alewife can suppress yellow perch during their pelagic phase is indirectly corroborated by apparent suppression by alewife of other species with pelagic larvae. Madenjian *et al.* (2008) argue alewife suppression affects four species: yellow perch, emerald shiner (*Notropis atherinoides*, in tributaries which alewife ascend to spawn), deepwater sculpin, and burbot. The two species with the most abundant larvae, deepwater sculpin and

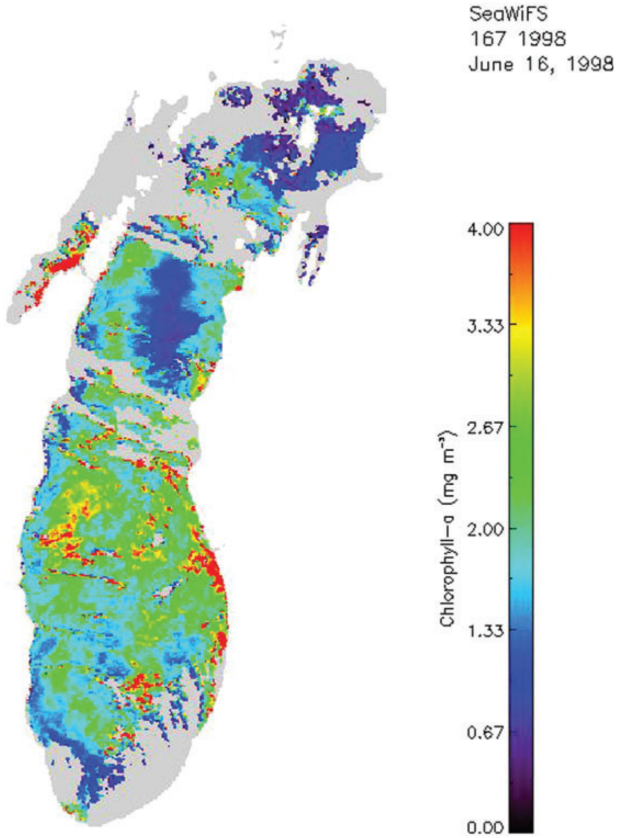

Figure 4. Sea WiFS estimated chlorophyll distribution in Lake Michigan about 2 weeks following a 160-kph wind event that destratified Lake Michigan on 2 June 2008 (Julian Day 154). The figure shows relative chlorophyll concentrations estimated from SeaWiFS. Pixel size is 1 km^2. The destratification increased annual primary production by an estimated 25% (Lesht *et al.*, 2002). The destratification occurred just before yellow perch and alewife spawning and may be responsible for large year classes for both species. Note the spatial heterogeneity.

burbot, both have marine relatives and both become demersal, so, because the alewife is an obligate planktivore, a negative relationship between recruitment and alewife abundance would argue for the larval phase critical period. Deepwater sculpin larvae (~9 mm) emerge in deep water before stratification (peak hatching in March) and are found both shallow (epilimnetic during stratification) and deep (thermocline and hypolimnetic during stratification) with a transition to becoming benthic at ~20–40 mm in July (Nash and Geffen, 1991; Geffen and Nash, 1992). Sources of burbot larvae (3–4 mm TL) range from tributary streams (late March) to offshore deep reefs (as late as June; Mansfield *et al.*, 1983; Nash and Geffen, 1991; Jude *et al.*, 2013) and the larvae are primarily shallow (epilimnetic after stratification, Nash and Geffen, 1991). At their peak, both deepwater sculpin and burbot can be at densities of hundreds per 100 m^3 (Nash and Geffen, 1991; Jude *et al.*, 2013). In the cases of burbot and deepwater sculpin, the larval phase critical period is analogous to those observed in marine environments. This perhaps not surprising, given their marine ancestors. Is there (for Lake Supeiror), and was there (for the other LGL-DEEP), a significant larval fish predator? We address this in the final narrative.

Narrative 3: is there an absence of native predator pressure on LGL larval fish?

In Narrative 2, we argued that when evolutionary time was "controlled" and spatial scale was varied, yellow perch appear to transition from a demersal, juvenile critical period to a larval pelagic critical period. However, the evolutionary time-scale may have been recently confounded by the addition of the alewife predator, which is of coastal marine origin. Other clupeids can induce a critical stage in their prey species via predation on early life stages, as exemplified by Atlantic herring impacts on Atlantic cod (Köster and Möllmann, 2000). Hence, the critical period for Lake Michigan yellow perch may have shifted from the juvenile to the larval stage due to the alewife invasion. Rainbow smelt, another marine-origin invader, may have similarly affected recruitment of cisco by feeding on cisco larvae. Stockwell *et al.* (2009) proposed that cisco recruitment failed in Lake Superior from the late 1950s to early 1980s as a consequence of rainbow smelt dominating the planktivore community. Only when rainbow smelt populations were greatly reduced, likely by recovering lake trout populations, were cisco able to produce a huge year class (in 1984); large year-classes have recruited periodically since then. Thus, the LGL may have been a safe haven for the development of prolonged larval phases over evolutionary time. The lakes lacked a native predator that could induce a larval critical stage in prey species; alewife and smelt have capitalized on the vulnerability of cisco and smelt that have not yet needed to evolve a shortened larval life stage

Figure 1 provides a conceptual framework for generating testable hypotheses regarding the interaction of spatial scale and evolutionary time-scale. Both the LGL-DEEP and Lake Baikal's fish fauna were largely founded by coregonines and cottoids, but in Lake Baikal there has been considerably more evolutionary time for fish with extended larval periods to evolve, with consequent potential for predation and defensive adaptation. Hence, we turn our focus to the pelagic fish of lakes Superior and Baikal, with additional reference to alewife in Lake Michigan. Because there is no main basin population of yellow perch in Lake Superior, a native predator or suite of larval fish predators most likely would be feeding on larval deepwater sculpin and burbot, two of the species that Madenjian *et al.* (2008) argued were negatively impacted by alewife.

In Lake Baikal, five of the ~30 cottoid species have pelagic larvae. These include two species of the bentho-pelagic genus *Cottocomephorus* (Cottidae), both of which have male-defended stone cavity nests, and two ovoviparous obligate pelagic species, *Comephorus baicalensis* and *C. dybowski*. The fifth species with pelagic larvae is the non-endemic *Cottus kessleri*. The remainder of the approximately two dozen Lake Baikal cottoids are benthic with benthic larvae (Sideleva 2003). The pelagic cottoid larvae are a significant component of the diet of adults of the omul (*Coregonus autumnalis migratorius*), an upper water column congener of the native pelagic ciscoes of the LGL-DEEP, and the two *Comephorus* species both of which live in deep water but undergo a diel vertical migration (DVM, Sideleva 2003). Whether predation on these larval fish leads to a larval phase critical period has not been studied.

We argue that alewife occupy a composite depth range during the season at which pelagic larval LGL-DEEP fish are most abundant, comparable with that of Lake Baikal's omul and *Comephorus* spp. During the period of stratification, alewife can be found either shallow (epilimnion) or deep (hypolimnion). Shallow alewife school by day and disperse mostly horizontally at night. Deep alewife (hypolimnetic or during the unstratified period) vertically migrate apparently in conjunction with the DVM of *Mysis* (Janssen and Brandt, 1980; Boscarino *et al*., 2010). Based on field hydroacoustic data and complementary laboratory experiments, Boscarino *et al*. (2010) argued that, at night, *Mysis* made excursions from a depth at which they were probably not visible up to a light level at which alewife could likely see them at short range. Presumably such excursions by *Mysis* were made for quick feeding bouts.

We now use the alewife and the three larval fish predators from Lake Baikal as models for considering what native LGL-DEEP fish might be larval fish predators (Figure 5). The native species most likely to occupy a niche similar to that of alewife is probably a combination of lake cisco and kiyi (*Coregonus kiyi*), the latter being one of the six endemic deepwater ciscoes (three now extinct) of the LGL-DEEP. Kiyi undertake a nocturnal ascent in pursuit of *Mysis* in Lake Superior (Jensen *et al*., 2006; Stockwell *et al*., 2010; Ahrenstorff *et al*., 2011). A third party in the diel interaction is a deepwater morphotype of lake trout (*Salvelinus namaycush*) called "siscowet" which ascends at night to feed on kiyi. The ensemble of *Mysis*-kiyi-siscowet typically have a vertical migration depth range of ~100 m. Kiyi and perhaps siscowet (or siscowet-like forms) were native to all four of the LGL-DEEP but are now found only in Lake Superior.

Kiyi is likely a sibling species of lake cisco and may even be a phylogenetic descendent specialized for DVM. Stockwell *et al*. (2010) and Ahrenstorff *et al*. (2011) found that lake cisco (*Coregonus artedi*) performed DVM in Lake Superior but not as great a magnitude as kiyi. Ahrenstorff *et al*. (2013) have found that the lake cisco is highly variable in its DVM among different lakes. So the relatively extreme vertical range for the DVM of kiyi appears to be an extension of the lake cisco's continuum.

Because a pelagic phase in freshwater fish is uncommon or short (Houde, 1994), if there is a lack of a significant native predator on planktonic larval fish in the LGL-DEEP, it is likely related to the resource being too transient for significant evolutionary pressure for predators to evolve. However, it may be that *Mysis* is sufficiently comparable with larval fish in size and depth distribution for native fish to adapt to feeding on larval fish as prey. Feeding on *Mysis diluviana* may place alewife at depths at which it might encounter larval LGL-DEEP fish. *Mysis* (up to ~20 mm) is larger than typical LGL-DEEP native microcrustacea (up to ~3 mm) and it is evasive, using a negatively rheotactic tail-flip startle response to suction feeding attempts. Both alewife and lake ciscoes switch

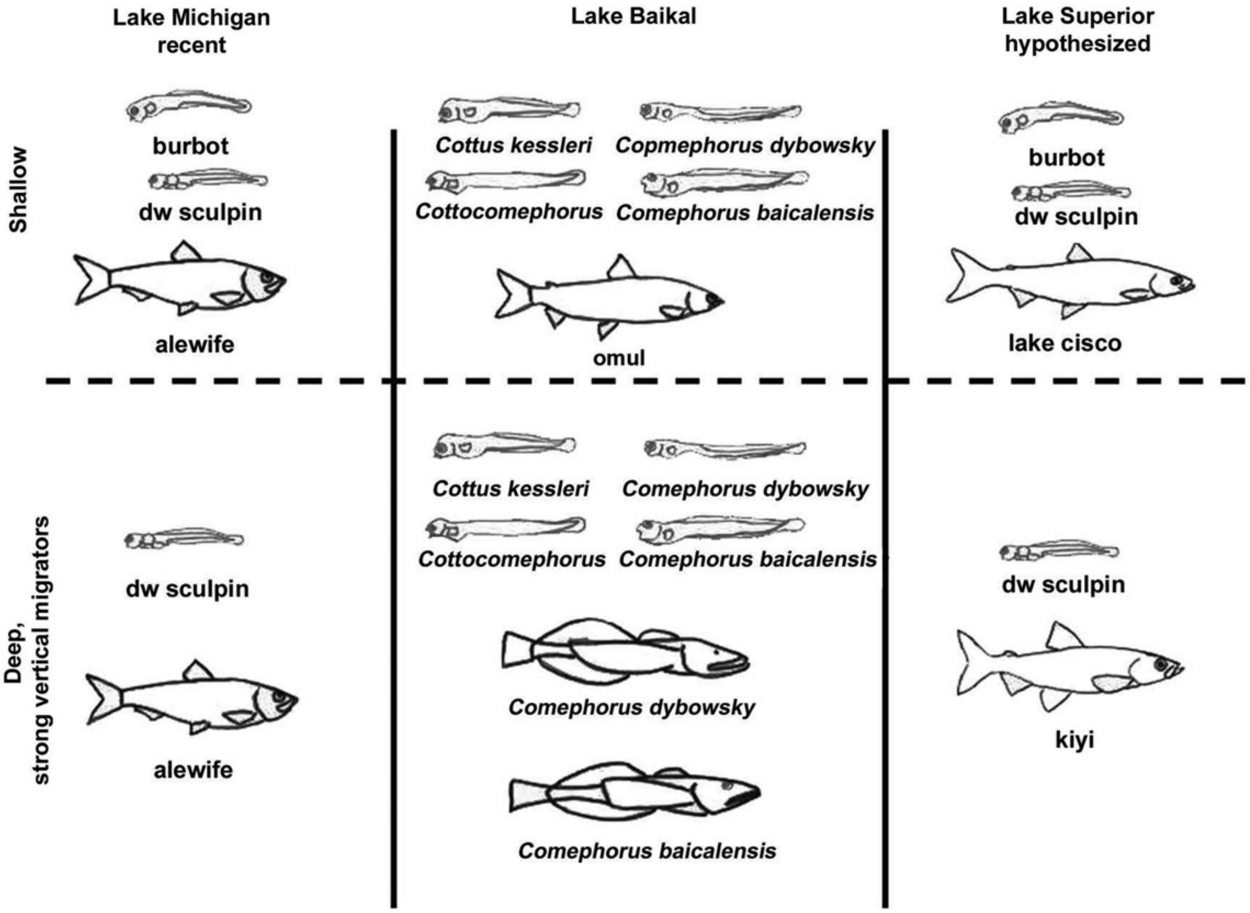

Figure 5. Larval fish predators in Lake Michigan (recent with the putative predator being the invasive alewife), Lake Baikal, and hypothesized for Lake Superior, based on Lake Michigan and Lake Baikal. Larval fish face left and predators face right. Surface predators have relatively little DVM, and deep predators tend to migrate in association with *M. diluviana* in Lake Michigan and Lake Superior and in association with *Macroheptopus* in Lake Baikal. See text for more details. Larval fish redrawn from Auer (1982) for the LGL and Sideleva (2003) for Lake Baikal. Adult fish redrawn from Hubbs *et al*. (2004) for LGL and Kozhova and Izmestiva (1998) for Lake Baikal.

from suction feeding to a ram feeding capture mode that neutralizes their feeding current for free-swimming *Mysis* (Janssen, 1978). An ability to feed on a relatively large and evasive zooplankter is a likely precondition for feeding on fish larvae which typically have well-developed evasive startle responses (see review by Fuiman and Magurran 1994). That alewife can feed on lake trout fry as large as 34 mm suggests that they are easily capable of feeding on the smaller larvae of yellow perch (4–5 mm at hatching), deepwater sculpin (9 mm at hatching), burbot (3 mm at hatching), and emerald shiner (8–10 mm at hatching).

Lake Baikal may have strong evolutionary pressures for pelagic larvae because, similar to LGL-DEEP lakes, it has a relatively small littoral zone compared with its vast pelagic zone, but has also had sufficient time for evolution of pelagic larvae from their benthic ancestors. Larval *Cottocomephorus grewinki* are available from late winter into autumn due to spawning in late winter, mid-spring, and late summer (Sideleva, 2003). These larvae are supplemented by larvae of the June/July spawning *C. kessleri*. But the major source of pelagic larvae is *C. baicalensis* which spawns all year, peaking in August/September, and *C. dybowski* which spawns from December to June, peaking in February/March (Sideleva, 2003). While the importance of larval fish in the diet varies seasonally, the per cent of the diet by mass in the omul can exceed 40% and the two species of *Comephorus* can consume ∼40% of their own production. In addition the two *Comephorus* species consume the pelagic larvae of *C. grewinki* and the benthic *C. kessleri* (Sideleva, 2003). Lake Baikal has a vertically migrating mysid-like pelagic gammarid amphipod, *Macroheptopus branickii* that is the major forage for adults of omul and *Comephorus* spp. so the larval fish predators have a year-round pelagic prey.

Because of a restricted seasonality of pelagic larval fish availability, LGL-DEEP larval fish cannot sustain alewife except perhaps seasonally. In deep water, *Mysis* likely sustains alewife and larval fish are commonly, perhaps mainly, incidental prey likely captured during the alewife nocturnal vertical migration. Boscarino *et al.* (2010) argued that, although alewife could feed in complete darkness on non-evasive prey via either ram filter feeding (Janssen, 1980) or directed attacks on individuals detected via the lateral line (Janssen *et al.*, 1995), they most likely detected *Mysis* visually because the upper extreme of the nocturnal *Mysis* distribution was at light intensities that allowed for short-range visual detection. It may be that a combination of sensory systems is used. What is potentially important for larval fish is that they are vulnerable to alewife predation both day and night. The lake cisco also can feed at night (Janssen, 1980), but, as far as is known the mechanism appears to be a non-selective pump filter feeding. So, our question whether there is a significant native larval fish predator and, if so, how it feeds, is unanswered.

Summary

The comparative approach is a classic means of testing evolutionary hypotheses, whether anatomical, physiological, behavioural, ecological, etc. Hjort (1914, 1926) conceived of "critical periods" in larval fish, but did not consider freshwater species. Houde (1994) subsequently introduced a comparative approach to early life histories of fish by contrasting freshwater vs. marine fish. We propose that, rather than creating a dichotomy between marine and freshwater fish, a deeper understanding of early life histories will derive from considering both systems in a continuum along temporal and spatial scales. Fish in small, shallow, short-lived freshwater lakes do not need to contend with currents that advect them into deep water, nor do they have scope for extensive vertical migrations, and fish have evolved long larval stages; recruitment is largely determined at the juvenile stage (Houde, 1994). Larger lakes support development of pelagic larval phases, and consequent exposure to pelagic and vertically migrating predators, similar to marine systems. Older systems such as Lake Baikal have evolved predators that exploit larval stages, but the young LGL lack such predators; instead, the invasion of marine-derivative alewife and smelt had devastating effects on a naïve larval community.

Acknowledgements

Thanks to Barry Lesht for contributing Figure 4, J. R. Strickler for challenging discussions, and G. R. Harbison, J. Craddock, and L. P. Madin for putting some salt in the blood of the senior author. J. R. Strickler, D. Garman, G. R. Smith, and anonymous reviewers offered insights and challenges. This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Oceanic and Atmospheric Administration, National Sea Grant College Program, and the State of Wisconsin. Federal grant number NA100AR4170070, project number R/FI-1. Crystal Lake yellow perch data were obtained from the North Temperate Lakes-Long-Term Ecological Research project database (NSF-#DEB-0822700).

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Handling editor: Howard Browman

ICES Journal of Marine Science

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ICES Journal of Marine Science (2014), 71(8), 2252–2267. doi:10.1093/icesjms/fsu080

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Review Article

Mechanisms driving recruitment variability in fish: comparisons between the Laurentian Great Lakes and marine systems

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Pritt, J. J., Roseman, E. F., and O'Brien, T. P. Mechanisms driving recruitment variability in fish: comparisons between the Laurentian Great Lakes and marine systems. – ICES Journal of Marine Science, 71: 2252–2267.

Received 11 December 2013; revised 7 April 2014; accepted 8 April 2014; advance access publication 27 May 2014.

In his seminal work, Hjort (in Fluctuations in the great fisheries of Northern Europe. Conseil Parmanent International Pour L'Exploration De La Mar. Rapports et Proces-Verbaux, 20: 1–228, 1914) observed that fish population levels fluctuated widely, year-class strength was set early in life, and egg production by adults could not alone explain variability in year-class strength. These observations laid the foundation for hypotheses on mechanisms driving recruitment variability in marine systems. More recently, researchers have sought to explain year-class strength of important fish in the Laurentian Great Lakes and some of the hypotheses developed for marine fisheries have been transferred to Great Lakes fish. We conducted a literature review to determine the applicability of marine recruitment hypotheses to Great Lakes fish. We found that temperature, interspecific interactions, and spawner effects (abundance, age, and condition of adults) were the most important factors in explaining recruitment variability in Great Lakes fish, whereas relatively fewer studies identified bottom-up trophodynamic factors or hydrodynamic factors as important. Next, we compared recruitment between Great Lakes and Baltic Sea fish populations and found no statistical difference in factors driving recruitment between the two systems, indicating that recruitment hypotheses may often be transferable between Great Lakes and marine systems. Many recruitment hypotheses developed for marine fish have yet to be applied to Great Lakes fish. We suggest that future research on recruitment in the Great Lakes should focus on forecasting the effects of climate change and invasive species. Further, because the Great Lakes are smaller and more enclosed than marine systems, and have abundant fishery-independent data, they are excellent candidates for future hypothesis testing on recruitment in fish.

Keywords: larval fish, Laurentian Great Lakes, life history, recruitment.

Introduction

Predicting year-class strength and subsequent recruitment have long been sought after to improve the management of fisheries (Houde, 2008). Hjort (1914) made several key observations to set the stage for a century's worth of fisheries research: (i) fish populations experience large fluctuations in abundance, (ii) year-class strength was set early in life, and (iii) egg production (i.e. the number of spawners) alone was insufficient to explain year-class strength variation. Stemming from these observations, much effort has been devoted to determining the factors that drive mortality of the early life stages of fish, particularly in marine systems (Houde, 2009). Much like the important marine fisheries that were the focus of Hjort (1914), freshwater fish in large lentic systems, such as the Laurentian Great Lakes, experience large fluctuations in recruitment. However, research into the dynamics of early life stages of fish in freshwater systems is comparatively newer than that for marine systems and it is unclear whether recruitment hypotheses derived from marine fish are transferable to Great Lakes fish and vice versa.

Marine and freshwater fisheries are often in stark contrast to each other. For example, marine fisheries are dominated by commercial users, whereas freshwater fisheries are often dominated by recreational users. Most obviously, marine fisheries are much larger in terms of spatial scale and the abundance of organisms and fishers than freshwater fisheries. However, the Laurentian Great Lakes (hereafter, Great Lakes) have many parallels to marine systems and, in some instances, are more analogous to marine fisheries than other freshwater fisheries. Although recreational angling is more prevalent, substantial commercial fisheries exist in each of the Great Lakes (Kinnunen, 2003). Similar to many marine fisheries, management of Great Lakes fisheries is international and occurs over multiple jurisdictional boundaries (GLFC, 1980). The Great

Lakes are much larger in size than most other freshwater systems and, though they are smaller than large offshore marine fisheries, they are affected by physical and biological processes similar to marine systems. The goal of this paper is to compare early life history paradigms between fish in Great Lakes and marine systems. Our objectives are to: (i) review the biological similarities and differences in early life stages between Great Lakes and marine fish, (ii) review the physical similarities and differences between Great Lakes and marine systems, (iii) review the factors driving recruitment in Great Lakes fish, and (iv) compare factors driving recruitment in Great Lakes fish to factors driving recruitment in Baltic Sea fish. Based on comparisons of recruitment processes between marine and Great Lakes systems, we recommend areas for continued research on the early life stages of fish in the Great Lakes, including determining the effects of climate change and invasive species on recruitment.

Biological similarities and differences between Great Lakes and marine species

Fish display tremendous variation in life history strategies (Winemiller and Rose, 1992; Winemiller, 2005); however, some differences can be generalized for Great Lakes and marine species. Many of the large-bodied Great Lakes fish are among the most fecund North American freshwater fish (Frimpong and Angermeier, 2009). For example, walleye (*Sander vitreus*), burbot (*Lota lota*), and white bass (*Morone chrysops*) can all have greater than 500 000 eggs per female. However, compared with morphologically similar marine species, such as Atlantic cod (*Gadus morhua*), walleye pollock (*Gadus chalcogrammus*), and striped bass (*Morone saxatilis*) (all species that can have over 1 million eggs per female), the large-bodied Great Lakes species have comparatively low fecundity. We compared fecundity, length at hatching, and pelagic or demersal egg location between a subset of commercially harvested Great Lakes species and a subset of commercially harvested species in the North Atlantic Ocean. Using commercial fishing catch records, we populated a list of 29 Great Lakes species (GLFC, 2013) and 23 North Atlantic species (NAFO, 2013) for comparison (Appendix 1). We limited our search to commercially important species because these species have well-documented life history information and they are the focus of recruitment research (below). For Great Lakes species, we obtained life history information from Frimpong and Angermeier (2009) and Auer (1982), and for North Atlantic species, we obtained life history information from Collette and Klein-MacPhee (2002). We tested for differences in fecundity and hatching length between Great Lakes and North Atlantic fish using Mann–Whitney *U*-tests and we tested for differences in demersal or pelagic egg orientation using Fisher's exact test. In general, Great Lakes fish are far less fecund than fish of the North Atlantic (Mann–Whitney *U*-test, $p = 0.002$) (Figure 1). The mean hatching length of the Great Lakes fish in our analysis (6.4 mm) was larger than North Atlantic fish (5.2 mm); however, this difference was not statistically significant (Mann–Whitney *U*-test, $p = 0.161$) (Figure 1). Furthermore, most Great Lakes fish have demersal eggs whereas North Atlantic fish have pelagic eggs (Fisher's exact test, $p < 0.001$) (Figure 1).

The differences in the biology between the early life stages of Great Lakes and marine species can potentially lead to differences in the factors that drive mortality at the egg and larval stages (Miller *et al.*, 1988). For example, the benthic eggs of Great Lakes species are subjected to predation for long periods of time (weeks to months) whereas the pelagic eggs of marine species are subjected to pelagic predators for much shorter times. Other sources of mortality at the egg stage, such as mechanical mortality, and the dispersal of eggs will also differ as a consequence of different position in the water column. In marine fish, the incubation period is much shorter and larvae are less developed at hatching than freshwater species. As a result, the larvae of marine fish generally have reduced performance (ability to swim, capture food, and avoid predators) compared with larvae of freshwater fish and mortality at the larval stage for marine fish is likely more acute than for freshwater fish (Houde and Zastrow, 1993; Houde, 1994). The higher survival of the larvae of freshwater fish may also lead to an increased importance of intraspecific interactions during the juvenile stage for setting year-class strength compared with marine fish (Houde, 1994).

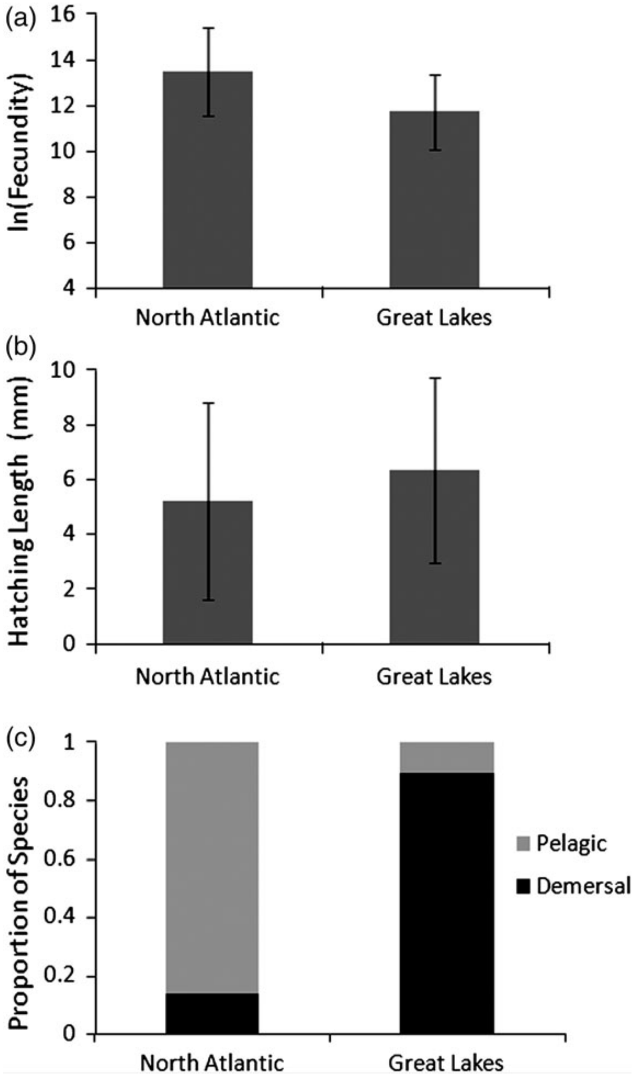

Figure 1. Mean (± SD) values for (a) maximum fecundity, (b) mean length at hatching, and (c) pelagic or demersal egg orientation for a subset of commercially important fish of the North Atlantic Ocean and the Laurentian Great Lakes.

Physical similarities and differences between Great Lakes and marine systems

The physical habitat in the Great Lakes and marine systems is similar in many aspects, making the Great Lakes more analogous to marine systems than other freshwater systems. For example, similar to ocean currents, the Great Lakes have large-scale patterns of water circulation (Beletsky *et al.*, 1999) that are capable of transporting the early life stages of fish over large geographic areas (Zhao *et al.*, 2009). However, in contrast to ocean currents, which are relatively stable and driven by large-scale processes such as the Coriolis effect, long-term currents in the Great Lakes are weak relative to short-term wind-driven currents that can be intense and unpredictable (Beletsky *et al.*, 1999) (Figure 2). Another physical similarity between Great Lakes and marine systems is that vertical stratification can occur and can control thermal and biotic conditions (Figure 2). Hence, many of the physical processes controlling thermal and hydrodynamic conditions facing the early life stages of fish are similar in Great Lakes and marine environments.

Although many similarities exist with respect to physical habitat, there are important differences between the Great Lakes and marine systems. The Great Lakes are often more enclosed than most marine systems, which could limit the exchange of resources and organisms with adjacent systems. Also, the Great Lakes are smaller than most marine systems, in terms of both area and depth. As a consequence of the smaller scale of the Great Lakes, habitat heterogeneity is greater in the Great Lakes than in marine systems and different habitats (nearshore vs. offshore) are in closer proximity and more intimately linked in the Great Lakes. However, the Great Lakes are more comparable in size to some enclosed and coastal marine systems. For example, Lake Superior, the largest Great Lake, has a surface area of 82 000 km^2 (US Census Bureau, 2012), approximately one order of magnitude less than marine systems such as the Baltic Sea (surface area ~415 000 km^2; Håkanson and Bryhn, 2008) and the North Sea (surface area ~750 000 km^2; OSPAR Commission, 2000). Further, Lake Superior has a deeper average depth (147 m; US Census Bureau, 2012) than the Baltic Sea (average depth ~61 m; Håkanson and Bryhn, 2008) or the North Sea (average depth ~95 m; OSPAR Commission, 2000). In contrast, outside of the Great Lakes, none of the largest freshwater lakes in the United States have surface areas >4000 km^2 (US Census Bureau, 2012). Hence, the Great Lakes are more similar in size to enclosed marine systems than they are to most other lentic freshwater systems.

In Great Lakes and marine systems, productivity can range from highly eutrophic to oligotrophic, and annual gross primary productivity (GPP) is similar between the Great Lakes and many marine systems. For example, Lake Superior, the most oligotrophic of the Great Lakes, has an annual rate of GPP of ~90 g C m^2 $year^{-1}$ (Sterner, 2010), Lake Michigan has an annual rate of GPP of ~250 g C m^2 $year^{-1}$ (Fahnenstiel *et al.*, 2010), and Lake Erie, the most eutrophic of the Great Lakes, has an annual rate of GPP of ~340 g C m^2 $year^{-1}$ (Fitzpatrick *et al.*, 2007). Similarly, Longhurst *et al.* (1995) estimated GPP for 72 regions across the world's oceans and found annual rates of GPP ranging from 71 g C m^2 $year^{-1}$ in oligotrophic, open-ocean areas to 730 g C m^2 $year^{-1}$ in eutrophic coastal areas, with a mean GPP of 267 g C m^2 $year^{-1}$ across systems. Hence, the annual rates of GPP in the Great Lakes are similar in magnitude to many other marine systems and as a result, the amount of energy available to primary consumers (zooplankton) and secondary consumers (larval fish) is likely comparable between the Great Lakes and marine systems.

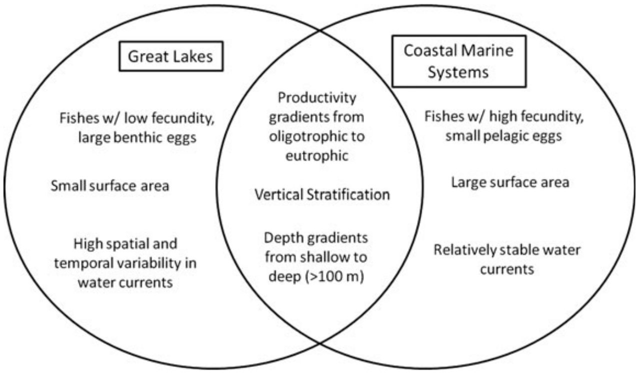

Figure 2. Physical and biological differences and similarities between Great Lakes and marine systems.

Anthropogenic impacts in Great Lakes and marine systems

Great Lakes and marine systems have similarities in some of their anthropogenic stressors. Overfishing has been widely documented in marine fisheries (e.g. Walters and Maguire, 1996) but has occurred in some Great Lakes fisheries (Brown *et al.*, 1999). Also, anthropogenic land use practices, such as urbanization and agriculture, have caused eutrophication and sedimentation of coastal marine systems (e.g. Lapointe and Clark, 1992) as well as coastal areas in the Great Lakes (Robertson and Saad, 2011). Although offshore marine ecosystems may be minimally affected by land use practices, coastal marine systems and Great Lakes systems face many of the same stressors stemming from urban and agricultural land uses.

Invasive species are a growing problem in marine systems (Molnar *et al.*, 2008); however, the Great Lakes have had more invasive species (more than 180 successful invasions; Mills *et al.*, 1994; NOAA, 2012) than most marine fisheries (0–74 invasions in coastal systems globally; Molnar *et al.*, 2008). Invasive species have altered physical habitats, foodweb structure, and energy flow in the Great Lakes. For example, dreissenid mussels have hardened benthic habitats and have changed the distribution of nutrients throughout the Great Lakes (Nalepa and Schloesser, 1993; Hecky *et al.*, 2004). Invasive fish such as sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) have also altered the structure of Great Lakes fish communities. Sea lamprey caused a collapse in some fish populations in the Great Lakes and alewife have become one of the most abundant forage species in the Great Lakes (Mills *et al.*, 1994). The Great Lakes have been invaded by species across many taxonomic groups and from several different areas, including species from the Atlantic Ocean, such as alewife and sea lamprey, and species from Eurasia, such as dreissenid mussels and round goby (*Neogobius melanostomus*) (Mills *et al.*, 1994).

In addition to the accidental introduction of non-native species, another contrast between the Great Lakes and marine systems is that many Great Lakes fisheries are made up of non-native species, generally Pacific salmonids, that are maintained through stocking (although some natural reproduction is known to occur). Non-native salmonids were originally stocked to reduce populations of invasive forage species (Tanner and Tody, 2002), but popular and economically valuable recreational fisheries for stocked salmonids have since developed (Dettmers *et al.*, 2012). Fish stocking programmes generally increase the abundance and richness of predators and can greatly affect aquatic ecosystems. Ramifications of fish stocking include altering foodweb structure and increasing top-down ecosystem controls (Eby *et al.*, 2006). In the Great Lakes, non-native salmonids compete with native predators, prey on native forage species, and have introduced diseases and parasites to native fish (Mills *et al.*, 1994). Hence, non-native salmonids, whose populations are maintained through continued stocking, may have a variety of direct and indirect effects on the recruitment of native fish in the Great Lakes.

Climate change is projected to influence both marine and Great Lakes systems, but the effects of climate change on fish populations may vary across species and systems. In the Great Lakes, warming temperature will lead to less ice cover (Smith, 1991) and more intense storm events that will affect water circulation and inputs of sediments and nutrients to the Great Lakes (Michalak *et al.*, 2013). Other predicted climate change effects on the Great Lakes include lower water levels, deeper or shallower thermoclines, and less dissolved oxygen in deepwater habitats (Smith, 1991; Magnuson *et al.*, 1997; King *et al.*, 1999). In marine systems, ocean currents may be disrupted, ocean acidification will increase, dissolved oxygen will be reduced, and sea levels will rise (Hoegh-Guldberg and Bruno, 2010), and many of these effects have already been observed. Climate change will have profound influences on Great Lakes and marine habitats used by the early life stages of fish and will likely have important implications to fish recruitment (Rijnsdorp *et al.*, 2009). However, the effects of climate change on recruitment in fish populations are likely to be complex and species-specific (King *et al.*, 1999). Furthermore, climate change may induce shifts in species distributions in marine systems (Roessig *et al.*, 2004) whereas the geographic confinement of the Great Lakes may limit the ability of species to shift in distribution (Sharma *et al.*, 2011). As a result, localized extinctions of species due to climate change may be more prevalent in the Great Lakes than in marine systems.

Influential recruitment hypotheses

Many hypotheses have been generated to explain the factors driving recruitment in fish. These hypotheses have been pioneered in marine systems and fall under one or more of three broad categories: (i) trophodynamic hypotheses that focus on lower trophic levels and subsequent food availability to early life stages of fish, (ii) hydrodynamic hypotheses that focus on transport of early life stages to (or away from) appropriate nursery habitats, and (iii) spawning-stock hypotheses that focus on the condition or behaviour of adults. Several of the most influential recruitment hypotheses are summarized in Table 1; for recent thorough reviews of recruitment hypotheses for marine fish, see Kamler (2005), Houde (2008), and Houde (2009).

Recent testing of recruitment hypotheses in the Great Lakes

We conducted a literature search using ISI Web of Knowledge to find studies that test recruitment hypotheses in the Great Lakes. We paired location keywords, including “Great Lakes”, “Lake Michigan”, “Lake Erie”, etc., with subject keywords such as “recruitment” and “year class”. Our criteria for including studies in our primary literature search were: (i) used some measure of year-class strength or recruitment as a response variable in a regression-based approach, (ii) based on empirical field observations (rather than those relying exclusively on laboratory or model data), and (iii) included at least 5 years of data to capture interannual variability. In our literature survey, we excluded studies that focused on the recruitment of stocked fish (i.e. salmonids). We hypothesized that, relative to marine fisheries, recruitment in Great Lakes fisheries will be driven less by food availability and more by predation on eggs and larvae and parental effects. Moreover, we expected to see stronger density-dependent effects in Great Lakes fisheries. We found 39 studies that sought to explain mechanisms driving recruitment and met our criteria for inclusion (Appendix 2). We noted whether studies linked recruitment to one or more of five mechanisms: (i) trophodynamics (i.e. bottom-up influences of lower trophic levels), (ii) hydrodynamics, (iii) interspecific interactions (predation or competition with other species), (iv) spawning-stock influences, including abundance, behaviour, or characteristics of spawners, and (v) temperature or other abiotic factors. We determined the most important factor based on the author’s description or statistical outputs.

We found studies examining recruitment in all five Great Lakes, with Lake Michigan being the most heavily studied and Lake Ontario being the least studied (Figure 3a). Studies were conducted since the 1980s, with most studies occurring since the year 2000 (Figure 3b). Yellow perch (*Perca flavescens*) was the most studied species followed by alewife and walleye (Figure 3c). Temperature, interspecific interactions, and spawning-stock influences were the most commonly cited drivers of recruitment (Figure 3d). Of the 39 studies, 6 tested hydrodynamic hypotheses, 20 tested interspecific hypotheses, 32 tested spawning-stock hypotheses, 21 tested the effects of temperature, and 13 tested trophodynamic hypotheses (many studies included multiple factors). Of the studies including temperature, 81% found this to be an important factor explaining recruitment of Great Lakes fish, 85% of studies including interspecific interactions found them to be important, and 91% of studies including spawning-stock characteristics found spawner influences on recruitment (Figure 3d). However, of the studies that tested hydrodynamic hypotheses, only 50% found that hydrodynamic processes were important to recruitment of Great Lakes fish and, of the studies including trophodynamic hypotheses, only 46% found lower trophic variables explained recruitment (Figure 3d). Specific findings from our literature search, along with additional supporting references, are described below.

Table 1. Influential recruitment hypotheses developed for marine fish.

Type	Author(s)	Hypothesis name	Hypothesized factors driving recruitment
Trophodynamic	Hjort (1914)	Critical period	Food availability at transition from endogenous to exogenous feeding
	Cushing (1990)	Match–mismatch	Food availability throughout larval stage
	Lasker (1978)	Stable ocean	Wind currents that promote ocean stratification and concentrate larvae and prey
	Anderson (1988)	Growth mortality	Larval growth, a function of food availability and temperature, controls survival and recruitment
	Cury and Roy (1989)	Optimal window	Wind currents that minimize advection and maximize larval-prey contact
Hydrodynamic	Hjort (1914)	Aberrant drift	Transport to or away from nursery areas by ocean currents
	Sale (1978)	Lottery hypothesis	Delivery by currents to coral reefs
	Iles and Sinclair (1982)	Member vagrant	Adults spawning in right place at right time to take advantage of appropriate currents
Spawning stock	Ricker (1954)	Stock–recruitment	Spawning-stock biomass controls recruitment through production and density-dependent controls

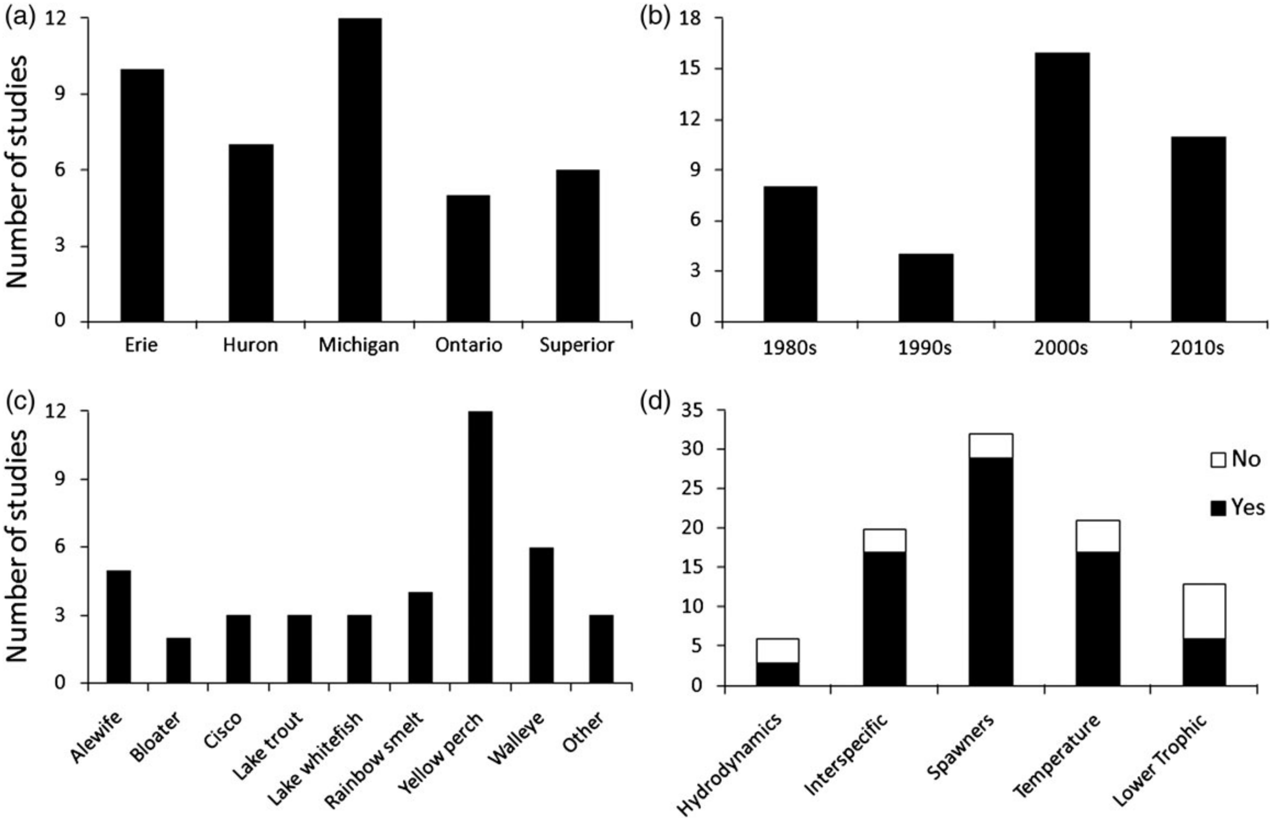

Figure 3. Summary of studies (39 total) describing recruitment mechanisms of Laurentian Great Lakes fish by (a) lake, (b) decade of publication, (c) species of interest, and (d) factors examined to explain recruitment variability and whether or not the authors identified a significant effect of those factors on recruitment.

Trophodynamic factors

Prey availability to larval fish has long been hypothesized as a driver of larval mortality and subsequent recruitment (Hjort, 1914) and some evidence exists that prey availability can influence recruitment in Great Lakes fish, although results from our literature search were mixed. In Lake Ontario, prey availability was positively correlated with larval growth and recruitment of lake whitefish (*Coregonus clupeaformis*) (Hoyle *et al.*, 2011) and higher total phosphorus (as a proxy for productivity) was positively related to alewife recruitment (O'Gorman *et al.*, 2004). Likewise, zooplankton density had a positive relationship with yellow perch recruitment in Lake Michigan (Dettmers *et al.*, 2003; Redman *et al.*, 2011; Weber *et al.*, 2011) and lake whitefish recruitment in Lake Michigan (Freeberg *et al.*, 1990). Greater productivity and zooplankton densities in a drowned river mouth connected to Lake Michigan produced better growth and survival of larval alewives than nearshore habitats of Lake Michigan, indicating that bottom-up factors can control alewife recruitment (Höök *et al.*, 2007). However, many Great Lakes researchers have found that zooplankton density is not a strong predictor of year-class strength (e.g. Ridgway *et al.*, 1990; Hoff, 2004a, b; Claramunt *et al.*, 2010) or larval mortality (Mason and Brandt, 1996), and others have found that bottom-up controls on zooplankton abundance are not prevalent drivers of year-class strength (Madenjian *et al.*, 2000). Bottom-up trophic controls on larval fish survival may therefore be important in some locations and for some species, but starvation mortality driven by lower trophic levels does not appear a universally important driver of recruitment in Great Lakes fish.

Food limitations can also lead to density-dependent mortality and growth of larval and juvenile fish. In the Great Lakes, density-dependent growth and survival of yellow perch has been documented in Lake Huron (Ivan *et al.*, 2011, Thayer *et al.*, 2007), however, walleye in Lake Huron did not exhibit density-dependent growth (Ivan *et al.*, 2011). Furthermore, no relationship between growth and recruitment was found for yellow perch in Lake Michigan (Fitzgerald *et al.*, 2004). Negative relationships between larval density and larval growth were also observed for lake whitefish in Lake Michigan (Claramunt *et al.*, 2010). Thus, it may be possible that production of larval fish can be greater than the capacity of the zooplankton food resource and lead to poor growth and reduced survival of larval fish.

Hydrodynamic factors

Water currents can transport the early life stages of fish long distances, and transport to appropriate nursery habitats can be crucial to larval survival in marine systems (Miller, 2007). In the Great Lakes, hydrodynamic processes may transport larval fish great distances and may also control mechanical mortality of eggs and larvae. For example, in Lake Erie, Zhao *et al.* (2009) used a bio-physical model to show that two weak walleye year-classes may have been driven by strong bottom currents, capable of causing egg mortality, and advection of walleye larvae away from nursery habitats whereas in strong recruitment years, bottom currents were gentle and larvae were transported to nearshore nursery habitats. However, hydrodynamic hypotheses have received little attention in the Great Lakes and support for the importance of hydrodynamics has been mixed. Hydrodynamic processes may be important to larval cisco (*Coregonus artedi*) in Lake Superior, which have been found to be transported by longshore currents from spawning grounds to nursery areas (Oyadomari and Auer, 2008). Similarly, high amounts of interannual variability in water currents in Lake Michigan can greatly affect the direction and distance of transport of larval yellow perch, which in turn can affect the thermal conditions the larvae experience and influence growth, settlement, and recruitment (Dettmers *et al.*, 2005; Beletsky *et al.*, 2007; Weber *et al.*, 2011). Other hydrodynamic processes such as river discharge (Mion *et al.*, 1998), and lake water levels (Henderson, 1985) may also influence egg and larval survival and recruitment.

Many studies have inferred that hydrodynamics are important to fish recruitment without explicitly including measurements or models of hydrodynamic processes. For instance, lake whitefish recruitment in Lake Michigan was positively related to spring wind intensity which possibly led to beneficial transport to nursery areas (Claramunt *et al.*, 2010). However, wind direction and intensity variables, serving as proxies for water movement and larval transport, failed to explain recruitment variability for lake whitefish in Lake Michigan (Brown *et al.*, 1993), yellow perch in Lake Michigan (Redman *et al.*, 2011), and walleye in Lake Erie (Zhao *et al.*, 2013). Overall, the effects of hydrodynamics on the early life stages of fish have only recently been quantified and although they have yielded new insights into recruitment variability of Great Lakes fish, further testing is warranted to fully understand how hydrodynamic processes influence recruitment.

Spawning-stock factors

Spawning-stock effects include biological attributes of the eggs or larvae resulting from the age, condition, or genetics of parents, or intraspecific interactions between spawners and progeny. Biological effects have been studied by several researchers in the Great Lakes. For walleye in Lake Erie, gizzard shad (*Dorosoma cepedianum*) abundance in autumn preceding spawning was positively related to recruitment of the following year-class, presumably by improving the energetic condition of adult spawners (Henderson *et al.*, 1996; Madenjian *et al.*, 1996). Furthermore, egg size increases with female walleye age, thus an older age structure of female walleye in Lake Erie may improve larval survival and recruitment (Venturelli *et al.*, 2010). Similarly, growth rate of adult yellow perch in Lake Erie preceding spawning was related to high recruitment, indicating that adult condition is important to recruitment (Tyson and Knight, 2001). Variation in bloater (*Coregonus hoyi*) recruitment in Lake Michigan can be explained by sex ratio as recruitment is negatively related to female predominance (TeWinkel *et al.*, 2002; Bunnell *et al.*, 2006), and sex ratio may also be important to explaining declining yellow perch recruitment in Lake Michigan (Marsden and Robillard, 2004); however, the exact mechanisms driving these relationships are unclear (Bunnell *et al.*, 2006).

Maternal effects on fecundity and the quality and morphology of eggs and larvae have been documented for many species throughout the Great Lakes. For example, maternal effects have been observed for egg size of walleye (Wang *et al.*, 2012), fecundity in Lake Michigan yellow perch (Lauer *et al.*, 2005), egg size of common carp (*Cyprinus carpio*) in Lake Michigan (Weber and Brown, 2012), and larval morphology and energy in Lake Michigan yellow perch (Heyer *et al.*, 2001). Timing of spawning and characteristics of females may also be important for explaining larval production in lake sturgeon (*Acipenser fulvescens*) (Duong *et al.*, 2011) and bloater in Lake Michigan (Rice *et al.*, 1987). Lake trout (*Salvelinus namaycush*) that rely on the invasive alewife as a primary food source are known to have a thiamine deficiency that limits the viability of eggs and following an alewife collapse in Lake Huron, lake trout were able to reproduce more successfully (Riley *et al.*, 2007), although the relationship between improved reproduction and recruitment is not clear (Fitzsimons *et al.*, 2010). Although most of these studies implicate recruitment effects, few have actually documented the influence of maternal effects on recruitment.

Intraspecific interactions between spawners and progeny have also been shown to lead to density-dependent recruitment. Lake trout recruitment in Lake Superior (age-7 fish) is negatively related to the density of spawners, indicating that density-dependent controls of adults on juveniles and subadults limit recruitment in that population (Richards *et al.*, 2004; Corradin *et al.*, 2008). Similarly, alewife year-class strength in Lake Ontario is positively related to adult abundance when adult population size is small but inversely related to adult abundance when adult population size is large (O'Gorman and Schneider, 1986). Cannibalism may also be an important parental effect for some species. For example, the invasive rainbow smelt (*Osmerus mordax*) has shown periods of alternating high and low recruitment consistent with cannibalism in Lake Superior (Hoff, 2004a; Gorman, 2007) and in Lakes Erie and Ontario (Henderson and Nepszy, 1989; Lantry and Stewart, 2000). Cannibalism has also been implicated in causing a negative relationship between spawner density and recruitment in cisco in Lake Superior (Hoff, 2004b; Rook *et al.*, 2012) and in alewife in Lake Ontario (Ridgway *et al.*, 1990; O'Gorman *et al.*, 2004). In contrast to the cannibalistic effects found in many populations, yellow perch recruitment is positively related to the number of spawners in Lake Erie (Henderson and Nepszy, 1988) and Lake Michigan (Forsythe *et al.*, 2012) and no negative feedback with high spawning-stock density was found in lake whitefish in Lake Michigan (Brown and Eck, 1993). Positive stock–recruitment relationships have also been observed for lake trout in Lake Huron (He *et al.*, 2012).

Interspecific factors

Interspecific competition and predation also appear important drivers of recruitment in the Great Lakes, and these community-level dynamics have been altered greatly by invasive species. For example, white bass recruitment declined after the invasion of the closely related white perch (*Morone americana*) in Lake Erie, likely because of competition between age-0 white bass and white perch for food resources (Madenjian *et al.*, 2000; Eckmayer and Margraf, 2004). Similarly, competition with white perch caused a decline in four forage fish species in Lake Erie (Gopalan *et al.*, 1998). Competition has also been implicated for reducing zooplankton size, leading to reduced growth and survival in Lake Michigan's fish community (Crowder *et al.*, 1987). Predation on cisco eggs, larvae, and juveniles by lake trout (Hoff, 2004b) and rainbow smelt (Stockwell *et al.*, 2009) limit the recruitment of that species in Lake Superior. Substantial predation on larval yellow perch by alewife has been documented and may limit yellow perch recruitment in Lake Ontario (Brandt *et al.*, 1987; Mason and Brandt, 1996) and Lake Michigan (Shroyer and McComish, 2000; Redman *et al.*, 2011). In Lake Huron, predation and competition by alewife on larval and juvenile walleye may have served to limit walleye recruitment and recent strong year-classes of walleye have been attributed to the alewife collapse in Lake Huron (Fielder *et al.*, 2007; Fielder *et al.*, 2010). In Lake Erie, predation by abundant adult walleye can cause weak year-classes of yellow perch and other forage species (Hartman and Margraf, 1993; Gopalan *et al.*, 1998) and predation by yellow perch on burbot eggs and larvae can reduce burbot recruitment (Stapanian *et al.*, 2010). Recruitment of alewife is also limited by predation from salmonids (Madenjian *et al.*, 2005). Further highlighting the importance of predation on early life stages to recruitment of Great Lakes fish, Reichert *et al.* (2010) found that recruitment was greatest in western Lake Erie for larval yellow perch that used river plume habitat, as the high turbidity of this habitat offers a refuge from predators.

In freshwater fish, the long incubation periods increase the vulnerability of the egg stage to predation relative to that in marine fish. Predation by benthic fish and crayfish may also be sufficient to limit production of cisco in Lake Superior (Hoff, 2004b), lake trout in Lake Ontario (Fitzsimons *et al.*, 2002), and lake trout in Lake Michigan (Claramunt *et al.*, 2005). In the St Clair River, which is part of the connecting channel between Lake Huron and Lake Erie, native and invasive benthic-feeding fish reduced lake sturgeon egg survival by an order of magnitude and could greatly reduce larval production (Nichols *et al.*, 2003). Similarly, substantial egg predation by crayfish and fish was observed on lake sturgeon spawning in a Lake Michigan tributary that could limit larval lake sturgeon production (Caroffino *et al.*, 2010). Although egg predation has been documented by many researchers, the effects of egg predation on eventual year-class strength and recruitment of Great Lakes fish is not clear.

Temperature and climatic factors

Climatic effects seem to be important for explaining recruitment variation in Great Lakes species, although the exact mechanisms are often unclear. For example, synchrony in recruitment across spawning stocks and vast spatial extents indicates that large-scale abiotic factors drive recruitment variation (Stockwell *et al.*, 2009; Bunnell *et al.*, 2010; Rook *et al.*, 2012). As suggested by many researchers, temperature is an important driver of recruitment through a variety of mechanisms, including controlling prey abundance, growth, and survival of larval fish. Many studies have linked temperature to fish recruitment in the Great Lakes, although most of those can only speculate on the exact mechanisms by which temperature controls recruitment. Warmer spring temperatures enhanced the growth and overwinter survival of cisco in Lake Superior (Hoff, 2004b) and improved growth and survival of bloater larvae in Lake Michigan (Rice *et al.*, 1987). Warm spring temperatures also lead to stronger year-class strength of alewife in Lake Ontario (O'Gorman *et al.*, 2004), yellow perch in Lake Michigan (Janetski *et al.*, 2013; Redman *et al.*, 2011), alewife in Lake Michigan (Madenjian *et al.*, 2005), rainbow smelt in Lake Huron (O'Brien *et al.*, 2012), and alewife in Lake Huron (Henderson and Brown, 1985). Similarly, faster spring warming rates improved recruitment of yellow perch (Henderson and Nepszy, 1988) and walleye (Madenjian *et al.*, 1996) in Lake Erie and warmer spring temperatures improved nest success in smallmouth bass (*Micropterus dolomieu*) in Lake Michigan (Kaemingk *et al.*, 2011). Although warmer temperatures appear to benefit many species, colder winter temperatures appear to benefit burbot recruitment (Stapanian *et al.*, 2010) and extended duration of winter ice cover may benefit lake whitefish in Lake Michigan by reducing egg mortality caused by removal during wind events (Taylor *et al.*, 1987; Freeberg *et al.*, 1990; Brown *et al.*, 1993).

Comparing recruitment between Great Lakes and Baltic Sea fish

To provide a marine contrast to recruitment of Great Lakes fish, we conducted a second literature search to find studies that test recruitment hypotheses in the Baltic Sea using the same methods and criteria as our Great Lakes literature search, described above. The Baltic Sea provides a useful comparison to the Great Lakes because it is semi-enclosed, contains species in families also found in the Great Lakes, such as Clupeidae, Salmonidae, Gadidae, and Percidae, and has a similar body of fish recruitment work as the Great Lakes. We identified 25 studies in the Baltic Sea that met our criteria for inclusion (Appendix 3). Of these studies, 5 tested hydrodynamic hypotheses, 20 included temperature effects, 9 tested interspecific interactions, 19 tested spawning-stock influences, and 8 tested lower trophic level dynamics (Figure 4).

Compared with the Great Lakes, more studies found hydrodynamic and lower trophic level factors to explain recruitment variability whereas a similar proportion of studies identified interspecific interactions, spawning-stock influences, and temperature as important factors (Figure 4). However, we tested for differences in the proportion of studies identifying each factor using Fisher's Exact tests, with a Bonferroni correction for multiple comparisons (for five comparisons, $\alpha = 0.01$) and found no significant difference between the Great Lakes and Baltic Sea in the proportion of studies that found hydrodynamic ($p = 0.18$), trophodynamic ($p = 0.09$), interspecific ($p = 1.00$), spawning stock ($p = 1.00$), or temperature ($p = 0.66$) to explain recruitment variability. Thus, based on the studies we examined, the Great Lakes and Baltic Sea are highly similar in the factors determined to drive recruitment in fish (Figure 5).

Discussion and areas for continued research

Based on our review, high variability in recruitment of Great Lakes fish appears ubiquitous, in agreement with the observations of Hjort (1914). Hjort (1914) proposed two competing hypotheses to explain this variation: (i) intensity of starvation of larval fish at the transition to exogenous feeding, driven by plankton blooms, sets year-class strength and (ii) drift of larvae to or away from appropriate nursery grounds determines year-class strength. In the Great Lakes, starvation driven by bottom-up dynamics does not appear a strong driver of larval survival, and Hjort (1914)'s first hypothesis is

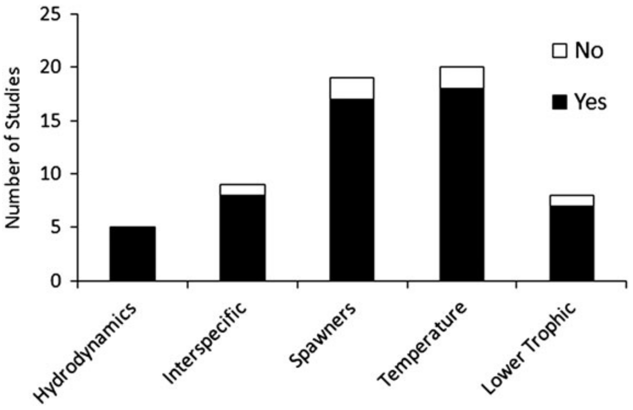

Figure 4. Factors examined to explain recruitment variability in Baltic Sea fish and whether or not the authors identified a significant effect of those factors on recruitment.

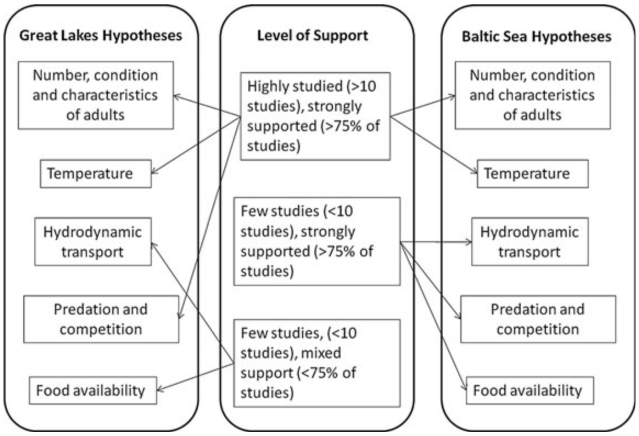

Figure 5. Number of studies and level of support for hypothesized drivers of year-class strength variability in Great Lakes and Baltic Sea fisheries.

not supported for most Great Lakes fish. Hjort (1914)'s second hypothesis has only recently received attention in the Great Lakes and although hydrodynamic processes do indeed appear important to some Great Lakes fish populations (Zhao *et al.*, 2009; Weber *et al.*, 2011), results have been mixed. Based on our review, Hjort (1914)'s hypotheses alone do not appear sufficient to explain recruitment variation in Great Lakes fish, similar to conclusions others have drawn for marine systems (e.g. Houde, 2008).

Many of the factors important to recruitment in Great Lakes fish in our review are the same factors important to recruitment in marine fish. For example, temperature has a profound influence on recruitment in Great Lakes and marine systems (Houde, 2008) and strong spawning-stock influences on recruitment appear ubiquitous in the Great Lakes and marine systems. In addition, our comparison in factors driving recruitment between the Great Lakes and the Baltic Sea show remarkable similarity between these two systems. However, our review shows some differences in the factors that drive recruitment in Great Lakes fish compared with similar reviews of marine fish (e.g. Houde, 2008, 2009). For example, food limitations at the larval stage driven by lower trophic level dynamics appear more prevalent in marine fish than in Great Lakes fish. Interspecific processes (competition and predation) have received more attention as factors determining recruitment of fish in the Great Lakes than for fish in marine systems (see also Myers *et al.*, 1997). However, our review from the Baltic Sea indicates that although interspecific interactions were considered in fewer cases than in the Great Lakes, they were highly significant in most of the studies that included them. From our review, it appears that the factors driving recruitment variability are often similar between the Great Lakes and marine systems and hypotheses may be transferable between systems with careful consideration of possible biological, physical, and anthropogenic differences.

Areas for continued research and opportunities for sharing

Several lines of research on recruitment in marine fish remain unexplored or underexplored in the Great Lakes. For example, the Stable Ocean Hypothesis (Lasker, 1978) and the Optimal Window Hypothesis (Cury and Roy, 1989) highlight the importance of stratification and microturbulence to larval fish feeding, growth, and survival. However, although some evidence exists to suggest that strong wind events reduce the survival of eggs and larvae in the Great Lakes (e.g. Zhao *et al.*, 2009), we found no examples that directly tested the Stable Ocean or Optimal Window hypotheses. Furthermore, the transport of eggs and larvae by currents, as proposed by Hjort (1914)'s second hypothesis, has recently been discovered as a strong driver of recruitment in marine fish (Miller, 2007) but in the Great Lakes, the testing of hydrodynamic hypotheses is in its infancy. We reviewed few studies that explicitly examined hydrodynamic factors, and the majority of those have only recently (<5 years) been conducted.

Since climatic variables are strong drivers of fish recruitment in Great Lakes systems and marine systems (Houde, 2008), climate change is likely to have a strong influence on future recruitment. In the Great Lakes, reduced ice cover and more intense storms (Smith, 1991; Magnuson *et al.*, 1997) will likely have a negative effect on fall-spawning species, such as lake whitefish, through increased mechanical mortality on eggs (Taylor *et al.*, 1987). Warmer temperatures may also negatively affect species with cold thermal preferences such as lake trout and burbot (e.g. Stapanian *et al.*, 2010), while positively affecting species with warmer thermal preferences such as yellow perch. As a result, species with warmer thermal preferences may increase in abundance while cold-water species may decrease. In addition, warming of the Great Lakes may leave them vulnerable to invasion by species that are tolerant of warm conditions (Mandrak, 1989). Research that predicts the response of recruitment to climate change (e.g. Jones *et al.*, 2006) and potential species invasions and range expansions could provide critical information for future management of Great Lakes fish.

As open-lake aquaculture systems become more prevalent in the Great Lakes (Yan, 2005), new stressors on fish recruitment may emerge. In marine systems, nutrient pollution has been shown to negatively affect surrounding ecosystems (Ackefors and Enell, 1994) and escaped organisms can reduce survival and reproductive success of wild stocks (Ford and Myers, 2008). In the Great Lakes, nutrient and organic matter pollution (Yan, 2005) and escaped organisms (Patterson and Blanchfield, 2013) may create similar problems. Research that seeks to understand the interactions between open-lake aquaculture and fish recruitment may be valuable to the management of fisheries alongside a growing industry.

Although research from marine systems has provided the foundation for testing recruitment hypotheses in the Great Lakes, the Great Lakes may be useful for informing marine research and management in the future. The Great Lakes have several attributes that make them excellent candidates for developing and testing fish recruitment hypotheses that could be applied to marine systems. First, the Great Lakes are smaller and more closed than most marine systems. Thus, fish populations in the Great Lakes will likely respond to climate change more quickly than marine fish populations and may serve as sentinels for valuable marine fisheries. Also, recruitment research in the Great Lakes has relied almost exclusively on fishery-independent data which is often lacking for marine fisheries (e.g. Walters and Maguire, 1996). This high-quality fishery-independent data collected in the Great Lakes will be useful for furthering fish recruitment research, particularly in response to changing environmental conditions.

The smaller size and enclosed nature of the Great Lakes are also likely to facilitate easier quantification and manipulation of fish habitats, fish population levels through stocking and management regulations, and water chemistry, such as nutrient inputs. As the emphasis on ecosystem-based management of marine fisheries continues to increase, research from the Great Lakes that has incorporated multiple species and habitats may serve as a guide to marine fisheries. Habitat and ecosystem-based management techniques have been regularly implemented in the Great Lakes, and the response of fish populations to management actions can be measured with more certainty. For example, management of predatory fish populations through stocking has been used to reduce forage fish populations (Dettmers *et al.*, 2012) and has had profound ecosystem-level effects in the Great Lakes (Eby *et al.*, 2006). Furthermore, interspecific interactions have been well studied in the Great Lakes, and the Great Lakes have a history of species invasions that are more intense than most marine systems. Invasive species have had many strong, negative interactions with native species (e.g. Madenjian *et al.*, 2000; Fielder *et al.*, 2007) and the response of Great Lakes fish to invasive species may provide insight into how marine fish may respond to future invasions. As species invasions continue to be problematic in marine systems (Molnar *et al.*, 2008), findings from the Great Lakes may be useful to guide future research in marine systems.

In addition to the parallels between the Great Lakes and marine systems, fish recruitment research in the Great Lakes may also be transferable to other large freshwater systems. As climate change, invasive species, pollution, and other anthropogenic stressors threaten fish populations in lentic systems around the world (e.g. Jeppesen *et al.*, 2012; Ostrovsky *et al.*, 2013), lessons from the Great Lakes may be used to guide research and management of fish in those systems. The Great Lakes may therefore be a useful system to advance recruitment research because of its similarities to both marine systems and other large freshwater systems.

Limitations

There are several important limitations to our review. First, we relied on the study design and conclusions of previous studies that may bias the conclusions of our review. For example studies designed to focus on narrow hypotheses were included and such studies may overlook important factors driving recruitment. For example, Marsden and Robillard (2004) concluded that yellow perch recruitment in Lake Michigan was driven by spawning-stock structure and not by alewife predation but later, more comprehensive work determined that alewife predation and prey availability were indeed important in explaining recruitment (Redman *et al.*, 2011). Moreover, much of the literature from the Baltic Sea focused only on stock–recruit relationships and did not consider other biotic and abiotic factors that could explain recruitment variability (e.g. Solari *et al.*, 1997). Next, the studies in our literature search that rely on time-series data and regression-based approaches often use indices of abundance to represent year-class strength and proxy independent variables to represent hypothesized important factors. For example, Zhao *et al.* (2013) used wind direction and velocity variables to represent hydrodynamic processes and these large-scale variables may not fully depict hydrodynamic effects on the early life stages of fish. In addition, proxy variables such as chlorophyll *a* and nutrient concentrations were sometimes used to model food availability (e.g. Fielder *et al.*, 2007), but these variables may fail to capture the availability of preferred zooplankton density (see also Crowder *et al.*, 1987). However, studies that used the densities of multiple zooplankton taxonomic groups often failed to draw a link between zooplankton dynamics and recruitment (Hoff, 2004a, b; Claramunt *et al.*, 2010). Finally, many of the conclusions drawn from the regression-based approaches were not determined from empirical measurements. For example, cannibalism is often implicated as an explanation of cyclical rainbow smelt recruitment (Lantry and Stewart, 2000), but these conclusions have generally been drawn without diet analysis of adult rainbow smelt. Hence, the exact mechanisms that control recruitment are often only inferred through correlative data in the field-based studies we analysed.

Conclusions

In accordance with the observations of Hjort (1914), year-class strength in the Great Lakes fisheries that we reviewed was generally highly variable, determined at early life stages, and not solely driven by the number or biomass of adult spawners. Thus, the observations that provided the foundation for recruitment research in marine fisheries ring true in Great Lakes fisheries. Similar to findings in many marine systems, our review showed that abiotic factors such as temperature and wind are strong drivers of recruitment. However, our review deviates from similar reviews of marine fisheries (Houde, 2008, 2009) in several key areas. For example, interspecific competition was found to be a strong driver of recruitment in many freshwater fish but interspecific interactions have received comparatively less attention in the recruitment in marine fish (Houde, 2008). The strong foundation of interspecific interactions in Great Lakes recruitment could serve to inform recruitment hypotheses for marine species, particularly in the context of invasive species and ecosystem-based management. Hypotheses and findings appear transferable between the Great Lakes and marine systems, but researchers should consider the inherent differences in the biology of fish, physical characteristics, and anthropogenic disturbances.

Acknowledgements

We thank C. Mayer for her insights that greatly improved this work. J. Fischer and anonymous reviewers provided comments that improved this manuscript. This article is Contribution No. 1847 of the US Geological Survey, Great Lakes Science Center and contribution No. 2014-06 of the University of Toledo Lake Erie Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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Appendix 1

Table A1. Maximum fecundity, mean hatching lengths, and egg orientation for current and historical commercially important species in the North Atlantic Ocean and the Laurentian Great Lakes.

System	Common name	Scientific name	Fecundity	Hatching length (mm)	Egg orientation
North Atlantic	Acadian redfish	*Sebastes fasciatus*	50 000	5.8	Internal
	Alewife	*Alosa pseudoharengus*	467 000	4.1	Pelagic
	American plaice	*Hippoglossoides platessoides*	2 200 000	5	Pelagic
	Angler	*Lophius americanus*	1 300 000	3.5	Pelagic
	Atlantic argentines	*Argentina silus*	28 000	7.5	Pelagic
	Atlantic cod	*Gadus morhua*	12 000 000	4.4	Pelagic
	Atlantic halibut	*Hippoglossus hippoglossus*	2 182 772	6.5	Pelagic
	Atlantic wolffish	*Anarhichas lupus*	37 920	18.5	Demersal
	Capelin	*Mallotus villosus*	50 000	6	Demersal
	Cusk	*Brosme brosme*	3 927 000	4	Pelagic
	Greenland halibut	*Reinhardtius hippoglossoides*	3 000 000	NA	Pelagic
	Haddock	*Melanogrammus aeglefinus*	3 000 000	3.5	Pelagic
	Herring	*Clupea harengus*	260 000	7.5	Demersal
	Mackerel	*Scomber scombrus*	1 980 000	3.2	Pelagic
	Pollock	*Pollachius virens*	4 000 000	3.6	Pelagic
	Red hake	*Urophycis chuss*	NA	2	Pelagic
	Roughhead grenadier	*Macrourus berglax*	25 000	NA	NA
	Silver hake	*Merluccius bilinearis*	391 700	3.1	Pelagic
	Skipjack tuna	*Katsuwonus pelamis*	1 331 000	NA	Pelagic
	Swordfish	*Xiphias gladius*	5 000 000	NA	Pelagic
	White hake	*Urophycis tenuis*	3 000 000	4	Pelagic
	Witch flounder	*Glyptocephalus cynoglossus*	3 000 000	4.9	Pelagic
	Yellowtail flounder	*Limanda ferruginea*	4 570 000	2.3	Pelagic
Great Lakes	Alewife	*Alosa pseudoharengus*	300 000	3.8	Pelagic
	Bigmouth buffalo	*Ictiobus cyprinellus*	750 000	5.7	Demersal
	Black crappie	*Pomoxis nigromaculatus*	188 000	3.5	Demersal
	Bloater	*Coregonus hoyi*	34 891	11.8	Demersal
	Bluegill	*Lepomis macrochirus*	50 000	2.9	Demersal
	Bowfin	*Amia calva*	64 000	5	Demersal
	Brown bullhead	*Ameiurus nebulosus*	13 000	7	Demersal
	Burbot	*Lota lota*	1 362 000	4	Pelagic
	Channel Catfish	*Ictalurus punctatus*	10 600	12.2	Demersal
	Cisco	*Coregonus artedi*	29 000	11.7	Demersal
	Common carp	*Cyprinus carpio*	2 000 000	3.3	Demersal
	Emerald shiner	*Notropis atherinoides*	8733	4	Demersal
	Freshwater drum	*Aplodinotus grunniens*	508 000	3.7	Pelagic
	Gizzard Shad	*Dorosoma cepedianum*	543 910	3.3	Demersal
	Goldfish	*Carassius auratus*	400 000	4.5	Demersal
	Lake sturgeon	*Acipenser fulvescens*	1 000 000	9.5	Demersal
	Lake trout	*Salvelinus namaycush*	11 500	15.2	Demersal
	Lake whitefish	*Coregonus clupeaformis*	415 000	11.2	Demersal
	Northern pike	*Esox lucius*	600 000	8	Demersal
	Rainbow smelt	*Osmerus mordax*	75 000	5.8	Demersal
	Rock Bass	*Ambloplites rupestris*	11 000	5.2	Demersal
	Quillback	*Carpiodes cyprinus*	63 779	6.4	Demersal
	Sauger	*Sander canadensis*	100 000	5.4	Demersal
	Smallmouth bass	*Micropterus dolomieu*	27 000	5.2	Demersal
	Walleye	*Sander vitreus*	600 000	6.9	Demersal
	White bass	*Morone chrysops*	1 000 000	2.3	Demersal
	White perch	*Morone americana*	150 000	2.3	Demersal
	White sucker	*Catostomus commersonii*	50 000	9	Demersal
	Yellow perch	*Perca flavescens*	100 000	6	Demersal

Appendix 2

Table A2. Studies describing factors controlling recruitment of Great Lakes fish.

Study	Lake	Common name	Most important factor	Secondary factors
Brown *et al.* (1993)	Michigan	Lake whitefish	Spawning stock	Ice cover
Bunnell *et al.* (2006)	Michigan	Bloater	Sex ratio	Temperature
Corradin *et al.* (2008)	Superior	Lake trout	Spawning stock	
Crowder *et al.* (1987)	Michigan	Multiple species	Competition	Larval growth rate
Fielder *et al.* (2007)	Huron	Walleye	Predation/competition	
Fitzgerald *et al.* (2004)	Michigan	Yellow perch	Unknown, not larval growth rates	
Fitzsimons *et al.* (2010)	Huron	Lake trout	Release of thiamine deficiency, maternal effects	
Forsythe *et al.* (2012)	Michigan	Yellow perch	Spawning stock	Predation and competition
Gopalan *et al.* (1998)	Erie	Multiple species	Predation	Competition, prey availability
Gorman (2007)	Superior	Rainbow smelt	Spawning stock (cannibalism)	Competition and predation
He *et al.* (2012)	Huron	Lake trout	Spawning stock	Predation by lamprey
Henderson (1985)	Huron	Yellow perch	Water level	
Henderson and Brown (1985)	Huron	Alewife	Temperature	
Henderson and Nepszy (1988)	Erie	Yellow perch	Temperature (warming rate)	Spawning stock
Henderson and Nepszy (1989)	Erie	Rainbow smelt	Spawning stock (cannibalism)	Predation, harvest
Hoff (2004a)	Superior	Rainbow smelt	Spawning stock	Rainfall, predation
Hoff (2004b)	Superior	Cisco	Spawning stock	Predation, temperature, wind
Hoyle *et al.* (2011)	Ontario	Lake whitefish	Prey availability	
Ivan *et al.* (2011)	Huron	Yellow perch and walleye	Density-dependent growth	Predation
Janetski *et al.* (2013)	Michigan	Yellow perch	Temperature	
Lantry and Stewart (2000)	Erie and Ontario	Rainbow smelt	Spawning stock (cannibalism)	
Madenjian *et al.* (1996)	Erie	Walleye	Adult condition	Spring warming rate, spawning stock
Madenjian *et al.* (2000)	Erie	White bass	Competition with white perch	Predation from walleye
Madenjian *et al.* (2005)	Michigan	Alewife	Predation	Temperature (+)
Marsden and Robillard (2004)	Michigan	Yellow perch	Foodweb alteration by zebra mussels	Sex ratio
O'Gorman and Schneider (1986)	Ontario	Alewife	Temperature	Spawning stock
O'Gorman *et al.* (2004)	Ontario	Alewife	Temperature	Predation, productivity
Redman *et al.* (2011)	Michigan	Yellow perch	Temperature	Competition, prey availability, spawning stock
Richards *et al.* (2004)	Superior	Cisco	Spawning stock	
Ridgway *et al.* (1990)	Ontario	Alewife	Predation	Spawning stock, temperature
Rook *et al.* (2012)	Superior	Cisco	Climate	Spawning stock
Shroyer and McComish (2000)	Michigan	Yellow perch	Competition and predation by alewife	
Stapanian *et al.* (2010)	Erie	Burbot	Predation by yellow perch	Temperature
Taylor *et al.* (1987)	Michigan	Lake whitefish	Spawning stock	Ice cover, temperature
TeWinkel *et al.* (2002)	Michigan	Bloater	Sex ratio	
Thayer *et al.* (2007)	Huron	Yellow perch	Density-dependence	
Tyson and Knight (2001)	Erie	Yellow perch	Adult condition	
Venturelli *et al.* (2010)	Erie	Walleye	Adult age structure	
Zhao *et al.* (2013)	Erie	Walleye	Spring warming rate	Spawning stock

Appendix 3

Table A3. Studies describing factors controlling recruitment of Baltic Sea fish.

Study	Species	Most important factor	Secondary factors
Axenrot and Hansson (2003)	*Clupea harengus*	Spawning stock, NAO	
Baumann *et al.* (2006)	*Sprattus sprattus*	Temperature	Spawning stock, bottom depth
Cardinale and Arrhenius (2000)	*Gadus morhua*	Spawning stock	
Cardinale *et al.* (2009)	*Clupea harengus*	Temperature	Spawner biomass and condition, zooplankton abundance
Gröger *et al.* (2007)	*Sander lucioperca*	Temperature	Fishing effort, salinity, NAO
Heikinheimo (2008)	*Gadus morhua*	Spawning stock	Reproductive habitat volume, salinity
Hudd and Kjellman (2002)	*Lota lota*	Acidic run-off	Temperature
Karas (1996)	*Perca fluviatilis*	Temperature	Winter starvation
Kjellman *et al.* (2003)	*Sander lucioperca* and *Perca fluviatilis*	Temperature	
Köster *et al.* (2001)	*Gadus morhua*	Spawning stock and egg production	Predation, transport, temperature
Köster *et al.* (2005)	*Gadus morhua*	Spawning stock and egg production	Prey availability, predation, transport, temperature
Köster *et al.* (2003)	*Gadus morhua* and *Sprattus sprattus*	Spawning stock	Oxygen, temperature, predation, prey availability
Lindegren *et al.* (2011)	*Clupea harengus*	Zooplankton abundance	Competition and predation, spawning stock abundance
Ljunggren *et al.* (2010)	*Perca fluviatilis*	Sprat biomass and zooplankton abundance	
MacKenzie and Köster (2004)	*Sprattus sprattus*	Temperature	
Mackenzie *et al.* (2008)	*Sprattus sprattus*	Temperature	
Mackenzie *et al.* (2012)	*Sprattus sprattus*	Temperature	Spawning stock
Mantyniemi *et al.* (2012)	Salmo salar	Predation	Prey availability (herring)
Margonski *et al.* (2010)	*Gadus morhua*, *Sprattus sprattus*, and *Clupea harengus*	Temperature	Spawning-stock biomass
Neuenfeldt and Köster (2000)	*Gadus morhua*	Spawning stock, cannibalism	
Raid *et al.* (2010)	*Clupea harengus*	Zooplankton availability	Spawning stock
Solari *et al.* (1997)	*Gadus morhua*	Spawning stock	
Sparholt (1996)	*Gadus morhua*	Spawning stock	Spawning habitat volume, predation
Ustups *et al.* (2013)	*Platichthys flesus*	Unknown	
Vallin and Nissling (2000)	*Gadus morhua*	Spawning stock characteristics	

Handling editor: Howard Browman

ICES Journal of
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ICES Journal of Marine Science (2014), 71(8), 2268–2280. doi:10.1093/icesjms/fst231

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics

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Persson, L., Van Leeuwen, A., and De Roos, A. M. The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. – ICES Journal of Marine Science, 71: 2268–2280.

Received 18 June 2013; accepted 9 December 2013; advance access publication 28 January 2014.

Food-dependent growth and size-dependent interactions form cornerstones in the dynamics of fish populations. Using two freshwater examples, we illustrate the importance of considering both these cornerstones for understanding system dynamics. Moreover, a proper understanding of the dynamics requires mechanistic linkages between individual-, population-, and community-level processes based on mass conservation principles. In one example, we further find that quantitative predictions of individual-level energy flows are essential for understanding the community dynamics. This mechanistic approach to understanding system dynamics is generally not reflected in fisheries models as an overview shows that only half of them incorporate food-dependent growth, and none fully observe the principles of mass conservation. As a marine example we examine patterns in the Baltic Sea system and show that no relationship between cod growth and sprat biomass is present related to the low size resolution in prey fish. Linking individual cod performance to its resource base is complicated by the many prey types cod uses over its life cycle. We conclude that an ecological perspective including size- and food-dependent processes is vital for ecosystem-based fisheries management making necessary a proper description of the interactive trophic structure as a result of mechanistic linkages between individual, population, and community processes.

Keywords: Baltic Sea, energy budget models, fisheries models, food dependence, ontogenetic niche shifts, physiologically structured population models, size structure, trophic configuration.

Introduction

Text books in ecology generally assume that the dynamics of populations are the result of mortality and reproduction only (Begon *et al.*, 1996; Turchin, 2003). In this definition, one basic aspect of the individual's life history—ontogenetic growth or development—is ignored, although ontogenetic growth is indeed a vital process, preceding reproduction by ensuring the energy allocation for the production of biomass. Fish provide an obvious example of the importance of individual development as individuals commonly increase in body weight over several orders of magnitude while developing from egg to mature individual (Werner and Gilliam, 1984). Moreover, the rate by which an individual fish grows is generally dependent on food availability, a fact long recognized and described by fish biologists (Beverton and Holt, 1957; Backiel, 1978). The pioneer paper by Hjort (1914) on the dynamics of fish populations also highlighted the changes and variability in individual growth of fish.

Fisheries management is mainly concerned with the biomass production of entire populations, which represent a collection of many individuals. Fisheries management approaches generally ignore the resource dependence of this production. Studies inspired by the dynamics of fish populations in freshwater lakes (cf. De Roos and Persson, 2001; Persson *et al.*, 2003, 2004), however, illustrate the potential of gaining a thorough insight in community regulation and functioning from models that consistently link population output (biomass production) to individual energy acquisition (food-intake). With its focus on stock production and its basis in single-species and age-structured models, marine fisheries management has traditionally incorporated these insights only to a limited extent. Following the research experience from trophic cascades in lakes (Carpenter *et al.*, 1987; Carpenter and Kitchell, 1993), increasing evidence now shows that also in marine communities changes at the top of the foodweb influence overall ecosystem dynamics: examples include the Black Sea (Daskalov *et al.*, 2007), the North West Atlantic (Frank *et al.*, 2005), and the Baltic Sea (Österblom *et al.*, 2006; Möllmann *et al.*, 2008). Understanding such community-wide changes requires an ecosystem-based management perspective that strives after an integrated assessment, considers the functioning of the entire ecological community (FAO, 2003; Christensen and Walters, 2004), and mechanistically accounts for the linkages between the individual, the population, and the community level. Such a general understanding, however, has been lacking so far for two main reasons: first, available data have been under-valued and little-used (e.g. changes in population size distributions are not incorporated in the estimates of reproductive capacity or spawning-stock biomass), and second, there has been a lack of particular and essential information that allows for an appropriate description of the trophic configuration to be studied. Where the first issue is possible to solve by turning around and taking an ecological perspective, the second part calls for a reconsideration of what kind of information is essential for developing an understanding of the dynamics of systems that are heavily influenced by size-structured interactions.

To illustrate in more detail the points made above, we first discuss two examples from freshwater systems, which both show that to understand the community dynamics it is essential (i) to consider the size- and food-dependent interactions and (ii) to mechanistically link processes at different levels (individual, population, community) of organization. The second example additionally shows that a proper quantitative handling of individual-level processes by using rather detailed physiologically structured population models (Metz and Diekmann, 1986; De Roos and Persson, 2001) may be necessary to gain an understanding of the dynamics of the system as a whole. Next, we discuss how the models that are commonly used for fish stock assessments and predictions for stock production with a focus on multispecies models account for the basic concept of resource-dependent development and biomass production and contrast this with assumptions of the aforementioned physiologically structured population models. Finally, we focus on the Baltic Sea system as a marine example, where we first consider the extent to which the data that are usually available for marine fish stocks can or cannot provide a sufficient basis for a more thorough ecological understanding. We point out that insufficient time resolution and especially resolution of size frequency in the data on both predatory as well as prey fish tend to prevent establishing a proper link between resource (prey) availability and consumer (predator) performance. Furthermore, we discuss the basic problem of deriving a proper trophic description of the dynamic interactions between different trophic components. We also point out that the amount of information necessary to yield an understanding of the dynamics of a specific system may turn out not to be as overwhelming as expected at first glance. Although it will be a far more complex task to provide the necessary ingredients for drawing similar links among organizational levels in freshwater systems as for marine systems, we highlight the ecological aspects that require more research and deeper investigations. A full consideration of food-dependent processes is essential for management purposes as food-dependent models yield different predictions about sustainable harvesting than do age-based models (De Roos and Persson, 2002; van Kooten *et al.*, 2010).

Linking individuals to populations and communities: experiences from freshwater lake systems

To examine how a (i) consideration of size and food dependence, (ii) linking of individual- and population-level processes, and (iii) correct quantitative predictions of individual-level mass flows can promote the understanding of fish communities, we will use two examples from freshwater systems. Our first example deals with a predator that feeds on a size-structured interspecific prey, whereas the other example considers a predator feeding on intraspecific prey (cannibalism) in which case the predator also shares the resource with its prey. In both examples, the community dynamics and structure over years have been characterized by high variations in both predator and prey population densities. For both examples, it also applies that a consideration of size and food dependence and a mechanistic linking of individual of population and community processes have been essential to unravel the mechanisms driving the dynamics of the systems.

Accounting for size and food dependence: the Takvatn system

Our first example considers changes in community structure over time as a result of the presence of alternative stable states. This empirical example relates to relatively recent theoretical developments that have shown that food-dependent development may give rise to stage/size-specific biomass overcompensation in response to mortality (i.e. increases in stage-specific biomass with increasing mortality), a phenomenon that cannot occur in unstructured or age-structured models (De Roos *et al.*, 2007; De Roos and Persson, 2013). Such overcompensatory biomass increases due to mortality have been experimentally demonstrated in many organisms, including fish (Schröder *et al.*, 2009; Ohlberger *et al.*, 2011). The presence of an overcompensatory biomass response to mortality leads to a 3-link (predator–consumer–resource) system that is prone to exhibit alternative stable community states. In the case when small juveniles in the consumer population are more efficient energetically than larger juveniles and adults, the consumer population will in the absence of predators suffer from strong resource limitation and very few smaller juvenile consumers will be present due to slow development of larger juveniles and a low reproduction rate among the adults. In contrast, if the predator is in the system and feeds selectively on small stages of the consumer (as is generally the case for piscivorous predators), its predation pressure will relax resource competition and lead to an increase in the biomass density and reproduction rate of adult consumers. This, in turn, leads to an increase in the biomass of the small stages of the consumer, although the predator is feeding on these small stages. Thus, the predator will through its predation activity cultivate its own prey leading to a situation where it may be able to sustain itself if present in the system but may not be able to invade the system (a scenario termed an Emergent Allee effect De Roos and Persson, 2002; De Roos and Persson, 2013). A state with both prey and predator present and a state with only a (stunted) prey population hence constitute the two alternative stable states of the community. Such a system is thereby also highly sensitive to harvesting-induced catastrophic predator collapses (De Roos and

Persson, 2002). In contrast, De Roos and Persson (2002; Figure 3) show that an age-based community description, in which the size-age relationship is constant and independent of changes in food availability does not allow for the overcompensatory biomass response and hence for the occurrence of the Emergent Allee effect.

A long-term whole-lake experiment in Lake Takvatn, northern Norway, provides experimental support for the presence of these two alternative stable states mediated via the mechanism described above. At the start of the experiment, the system was totally dominated by a stunted Arctic char (*Salvelinus alpinus*) population and the predator brown trout (*Salmo trutta*) was virtually absent from the system (Figure 1a; Persson *et al.*, 2007). A heavy fishing on the Arctic char population for 5 years as a result of management decisions resulted in a decrease in the total yield of Arctic char and a recovery of the brown trout. This recovery has also been sustained for more than 20 years after that the removal of Arctic char took place providing strong support for the presence of alternative stable states in this system (Figure 1a).

Understanding the dynamics of this system relies on a consideration of (i) the linkages between individual, population, and community levels and (ii) food and size dependencies in interactions. The heavy reduction in the population size of Arctic char resulted in a substantial increase in the growth rate and maximum size of Arctic char (individual-level response, Figure 1c). This increased growth of Arctic char, which has been sustained after the termination of the heavy fishing, resulted in a drastic shift in the size distribution of Arctic char: the abundance of large Arctic char increased and, most importantly, also the abundance of the smallest size classes of Arctic char increased as a result of increased population fecundity (population-level response, Figure 1b). In turn, this increase in the abundance of small (<15 cm) Arctic char, on which brown trout feeds (measured as the encounter rate, see Supplementary material for calculations), had a positive effect on the performance (condition) of brown trout (individual-level response, Figure 1d). Finally, the increased performance of brown trout resulted in the recovery of the brown trout population exerting a strong thinning effect on small Arctic char (individual to community linkage) leading to the sustenance of the high growth rate of Arctic char (community to individual linkage; Figure 1). Recent analyses of the Takvatn system also shows that variation in the individual growth rate of Arctic char during the post thinning phase is largely explained by intraspecifc density (Persson *et al.*, 2013).

It is apparent from the above that the understanding of the dynamics of the Takvatn system relies heavily on a consideration of food-dependent growth and explicit linking of processes at different levels (i.e. Figure 1). The fact that the increased performance of brown trout was dependent on the abundance of small Arctic char further shows the necessity of considering the size dependence of interactions. This conclusion is also supported by analyses of the relationship between brown trout performance (body condition) and total Arctic char biomass that show no relationship or even a negative relationship between brown trout condition and Arctic char biomass (Persson *et al.*, 2013). Data on total biomass of prey fish are thus clearly insufficient for linking prey availability to predator performance.

Quantitative predictions of individual-level mass flows: cannibalistic dynamics in Abborrtjärn 3

Although the above example illustrates how consideration of size and food dependence and linkages between different levels of organization are essential for understanding community dynamics, the comparisons between model predictions and empirical data were qualitative rather than quantitative. In contrast, our second example dealing with the dynamics of a cannibalistic fish population of perch (*Perca fluviatilis*) in Lake Abborrtjärn, northern Sweden, will show that correct quantitative predictions of individual-level mass flows are in this case necessary to understand the dynamics.

To mechanistically link different levels of organization in the Takvatn system, the use of physiologically structured population models (Metz and Diekmann, 1986; De Roos *et al.*, 2008), which predict population dynamics as the emergent result from processes taking place in the life history of individual organisms, has been essential. At the core of such population models is the description of the individual state dynamics by a dynamic energy budget (DEB) model (Persson *et al.*, 1998; Claessen *et al.*, 2000). This core DEB model implements a consistent cycle of energy flows and imposes strict mass conservation: energy assimilated from food intake is used for growth and maintenance (metabolism) of body mass or for reproduction, which are hence food-dependent. Alternatively, when reproduction only occurs annually it depends on body condition (Persson *et al.*, 1998), making this biomass output dependent on previous energy input. Thus, a consistent link between energy input into the system, in terms of biomass intake, and energy output from the system, in terms of biomass production, is realized. This modelling philosophy has been implemented in detailed, continuously structured population models, as well as in their more simplified, stage-structured analogues, which contain a discretized separation of different life stages (De Roos *et al.*, 2008; Van Leeuwen *et al.*, 2008).

For the cannibalistic perch system, the intake rate of the individual is a result of the consumption of resources shared by cannibals and victims and consumption by cannibals of victims. The first relationship has generally been characterized by a hump-shaped attack rate function of the form shown in Figure 2a assuming a fixed size of the resource (a derivation of this function including the biological basis for it is given in Persson *et al.*, 1998). In contrast, for the functional relationships between cannibals and victims, variation in both cannibal as well as victim size will have to be considered. In the fish ecology literature, the predation rate of piscivorous predators is generally viewed as being constrained by a lower prey–predator size ratio below which the piscivore cannot detect the prey fish and an upper prey–predator size ratio above which the prey fish escapes the piscivore (Lundvall *et al.*, 1999; Claessen *et al.*, 2000; Juanes, 2003). Within the range of predator and prey fish sizes where the predation rate is positive—the predation window—the predator's attack rate on differently sized victims for a specific predator length can be assumed to increase with victim size from zero at the lower size boundary to an optimum, to thereafter decrease again to zero at the upper size boundary (Claessen *et al.*, 2000). Figure 2b shows a two-dimensional illustration with empirical data for perch inserted. Along the optimal cannibal–victim size ratio, it can be further assumed that the attack rate increases with cannibal size according to a power function yielding the three-dimensional graph shown in Figure 2c (for derivation of functional relationships including the biological basis for these, see Supplementary material). To complete the description of the DEB model for the cannibalistic perch system, additional functional relationships for metabolic rates, food conversion, and allocation of ingested energy to reproduction and somatic growth, respectively, have to be derived (e.g. Persson *et al.*, 1998; Claessen *et al.*, 2000).

Both experimental and modelling analyses have shown that the dynamics of the studied cannibalistic populations is characterized

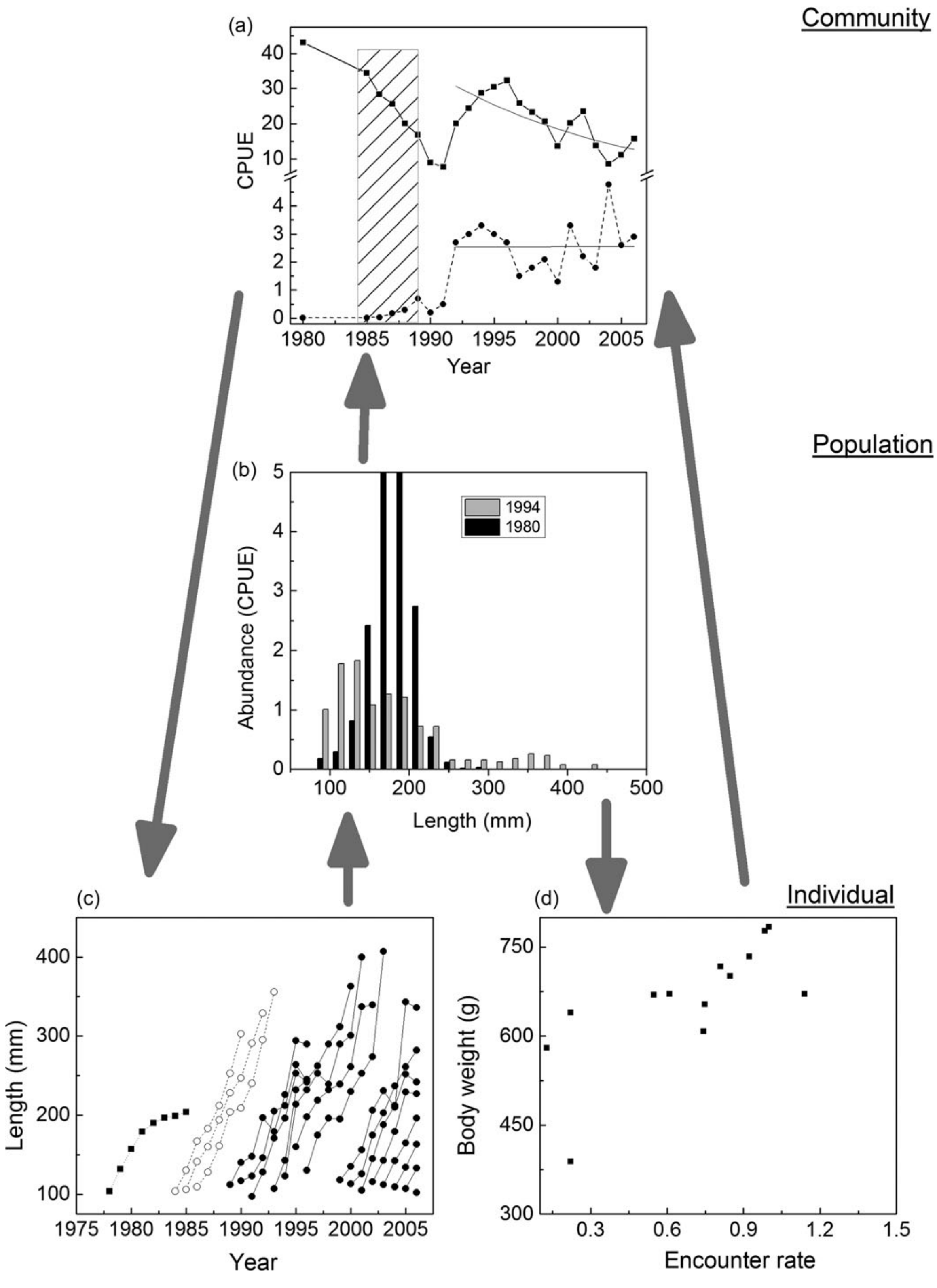

Figure 1. Different levels (individual, population, community) of organization in the Takvatn system including major linkages (grey arrows) between the different levels. (a) Changes in the abundance (cpue) of Arctic char (squares, solid line) and brown trout (circles, dashed line) in Lake Takvatn 1980 – 2006. Inserted thin solid curves starting in 1991 are trend lines. Hatched area represents the years with Arctic char thinning. (b) Abundance (capture per gillnet per 24 h, cpue) of difference size classes of Arctic char in Lake Takvatn before (1980, black histograms) and after (1994, grey histograms) the Arctic char thinning. (c) Individual growth rates of Arctic char before (filled squares, dotted line), during (open circles, dashed lines), and after the thinning (black circles, solid lines). (d) Relationship between the estimated encounter rate of a 400-mm brown trout with Arctic char and brown trout condition (g). See Supplementary material for estimation of encounter rate. Data from Persson *et al*. (2007).

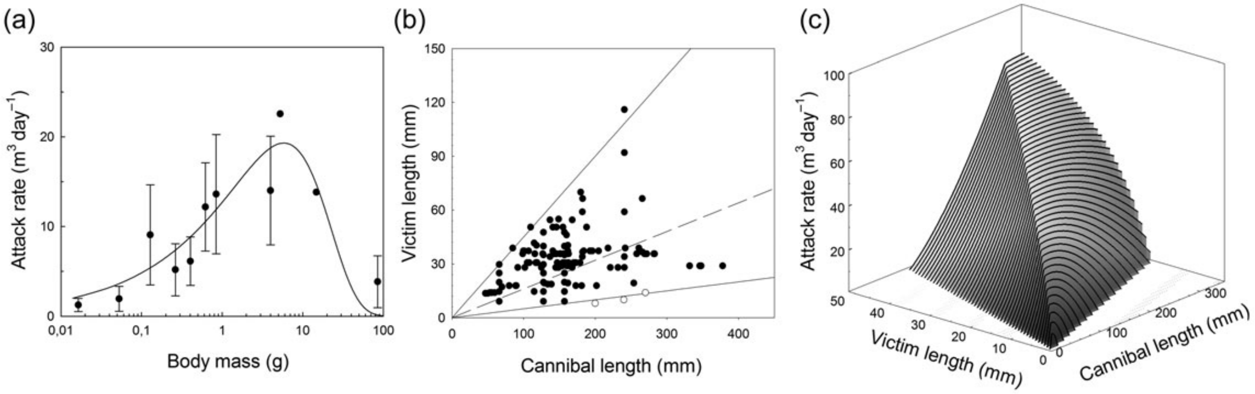

Figure 2. (a) Fitted relationship between the attack rate of perch on zooplankton and zooplankton resource density (*Daphnia* 1 mm). (b) Lower and upper size boundaries (solid lines) of the predation window for perch. The dotted line represents the optimum prey size for a specific predator size. Filled circles are empirical data points of observed prey sizes eaten by perch of different sizes based on field data or experiments. Open circles are results from experiments where perch did not attack the prey fish. (c) Three-dimensional plot of the attack rate (m^3 d^{-1}) of cannibalistic perch as a function of cannibal and victim sizes. Parameter values were $\delta = 0.05$, $=0.16$, $\varepsilon = 0.45$, $\beta = 0.4$, $\sigma = 0.6$. Data from De Roos and Persson (2013).

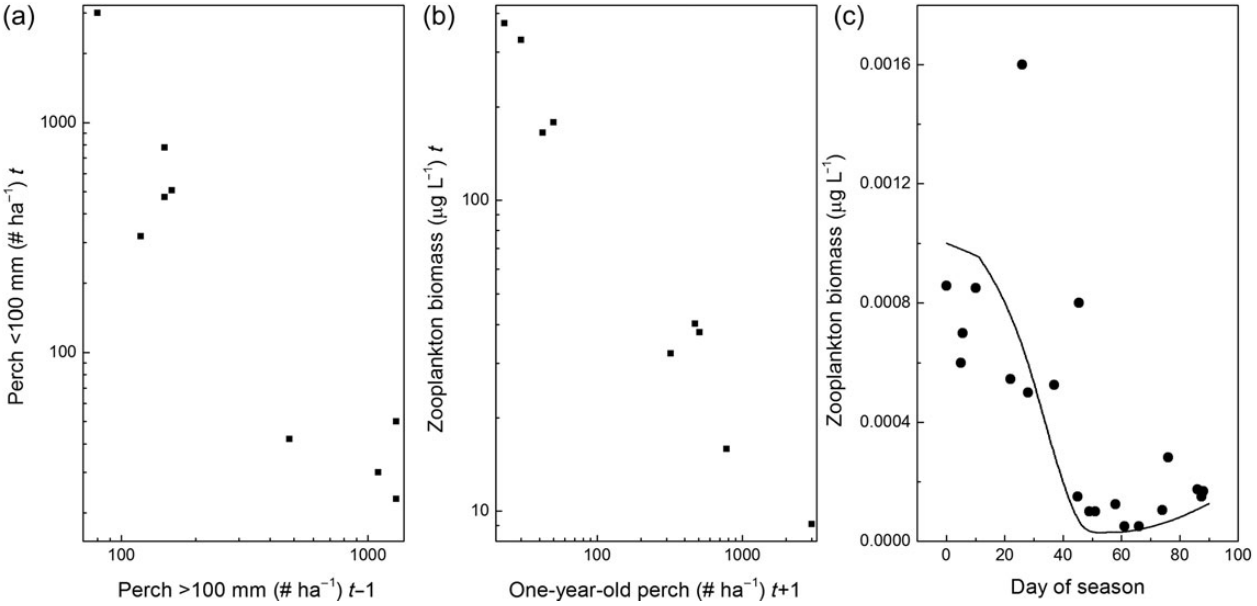

Figure 3. (a) Relationship between observed density of perch $<$100 mm and the density of perch $>$100 mm the previous year. (b) Relationship between zooplankton biomass (average of $\geq$3 samples for the period July – August) and the density of 1-year-old perch the following year. Densities of 1-year-old perch in year $t+1$ are taken as a measure of YOY perch densities in year t. (c) Predicted seasonal dynamics of the zooplankton resource during the giant phase (solid line). Superimposed on model predictions are the observed zooplankton biomasses in different years (filled circles). Data from Persson *et al.* (2003, 2004).

by high amplitude dynamics that can be separated into two phases (Claessen *et al.*, 2000; Persson *et al.*, 2000a, 2003, 2004). One (stunted) phase is characterized by high densities of cannibals imposing a high mortality on cannibalistic prey leading to low survival and low densities of 1-year-old perch the following year, a small asymptotic size of cannibals, and high biomasses of zooplankton. The other (giant) phase is characterized by low cannibal density leading to higher survival of cannibal prey and large number of 1-year-old perch the following year, a large asymptotic size of cannibalistic individuals, and low biomasses of zooplankton (Claessen *et al.*, 2000; Persson *et al.*, 2000a, 2003, 2004; Figure 3a and b).

Model predictions for young-of-the-year (YOY) perch mortality including the seasonal variation match well with the empirical observations regarding YOY perch mortality in the different phases (Persson *et al.*, 2004). Importantly, the lower mortality rate of YOY perch in the giant phase was not simply a result of the difference in cannibal density, but also due to a difference in the mean size of cannibals (which was higher in giant phase delaying the onset of cannibalism) and the increase in YOY perch size over the season. Detailed modelling of within season dynamics shows only a minor impact of perch consumption on zooplankton biomass in the stunted phase. In contrast, there is a strong impact of perch predation on the zooplankton resource during the giant phase (Figure 3c).

We next consider the question whether we can connect population level patterns (i.e. Figure 4a) to individual-level performance of the predator (food intake and growth of cannibalistic perch). In contrast to the Takvatn example, we will ask whether we can quantitatively predict both the diet and the growth of individual perch taking all ecological feedbacks into consideration. For illustration, we choose a perch of a size of 189 mm and compare the predicted and observed diets during the stunted and giant phase (a more extensive discussion of this analysis is given in Persson *et al.*, 2004). The diet during the stunted phase was mainly dominated by macroinvertebrates while zooplankton feeding and cannibalism were only observed to a smaller extent (Figure 4a). Macroinvertebrates also constitute the main part of the diet during the first 30 d of the growth season in the giant phase. After this date, the perch switches to feed mainly as cannibals (Figure 4b). For all prey items, there is a high agreement between predicted and observed diets (Figure 4a and b). Furthermore, it is worth noting that the high cannibalistic mortality of YOY during the stunted phase is associated with a low incidence of cannibal prey in the diet of potential cannibals, whereas the lower cannibalistic mortality of YOY during the giant phase is associated with a high incidence of cannibal prey in the diet. However, paradoxical at first sight, this pattern makes perfect sense when considering the dependence on the victim size of energy return for cannibals: during the stunted phase, almost all YOY perch are cannibalized before each individual victim represents any significant energy package for the cannibal; in contrast, cannibalism during the giant phase occurs over the whole growth season resulting in victim prey dominating the diet of cannibalistic perch from day 30 (early July) of the growth season.

Predicted and observed growth rates of perch differed substantially between the stunted and giant phases (Figure 4c and d). The difference in the growth rate between phases occurred for perch size >100 mm and is more or less entirely due to the consumption of cannibalistic prey. For both the stunted and the giant phase, predicted growth rates are also quantitatively in close agreement with observed growth rates (Persson *et al.*, 2003). This close match between predicted and observed growth rates of cannibalistic perch is essential to yield an appropriate estimate of population fecundity and thereby the overall cannibalistic population dynamics (i.e. the presence of the oscillation with two distinct phases depends on food dependence in both intake and reproduction). More specifically, the increased individual growth of cannibalistic individuals in the giant phase is essential to compensate for their small numbers and allows them to produce several strong YOY perch cohorts that in turn outcompete 1-year-old perch (previous year's YOY cohorts; Persson *et al.*, 2003). Without such a quantitatively correct prediction of individual growth rates—a result of a full handling of all rates—the model would not have predicted the sustained giant phase with its effect on overall foodweb structure of the system (Figure 3; Persson *et al.*, 2003).

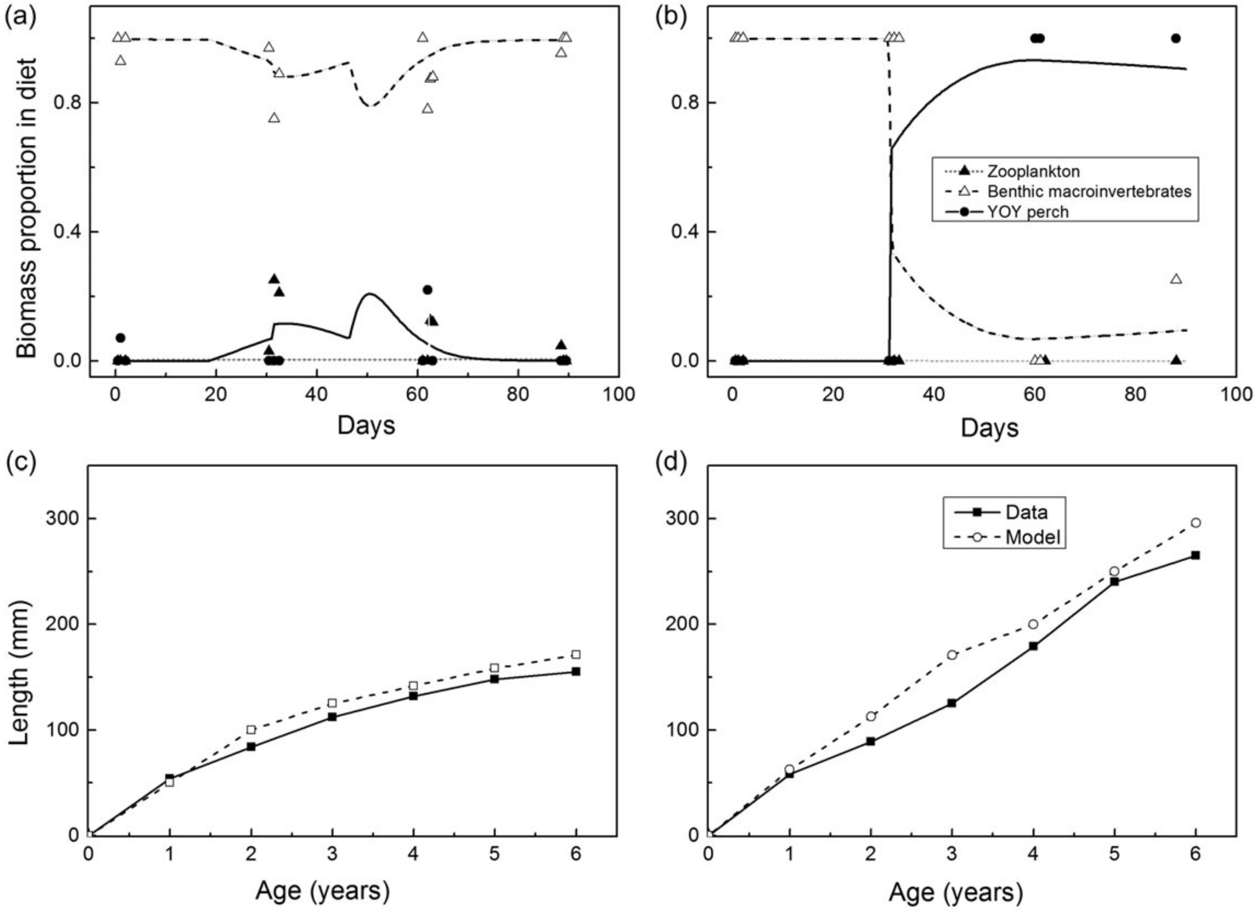

Figure 4. Predicted (lines) and observed (symbols) diets (biomass proportion) of perch over the season with an initial size in spring of 189 mm during the stunted (a) and giant phase (b) in Abborrtjärn 3. Observed data for the stunted phase include 1992, 1993, 1999, 2000, and that of the giant phase 1994 – 1997. Each data point represents the mean of >10 individuals. Model predictions and observed growth rates for perch during the stunted (c) and giant (c) phases. Data from Persson *et al.* (2003, 2004).

Conclusions

We have presented two examples, one of which focused on community structure and one of which focused on population dynamics. Both studies show that a sufficient size resolution in the description of prey fish and a consideration of food-dependent growth are essential to successfully establish links between processes and patterns and thereby allow for the prediction and understanding of population and community dynamics based on individual-level processes. In the Takvatn example, we furthermore showed that collapsing the description of a size-structured prey into a single point measure such as total biomass will generally lead to a failure in establishing the links between size-structured predators and size-structured prey at individual, population, and community levels. The detailed individual-level information that allows for a full accounting of individual-level mass flows and thereby quantitative predictions of piscivore performance, as exemplified by the perch system, is so far available for a restricted set of fish species constellations only (Persson and Brönmark, 2002; Persson *et al.*, 2004). Still, studies of these relatively few species constellations, which also include more complex trophic configurations (Persson, 2011), have helped us substantially in advancing our general conceptual understanding of the dynamics of freshwater fish populations and communities in general. These insights have also proven useful in the recent development of models for marine species such as herring and sprat and cod (Huss *et al.*, 2012; van Leeuwen *et al.*, 2013).

The Takvatn example also suggests that in some cases and for some type of questions only a relatively limited amount of information may be required to unravel the underlying processes that cause major changes in community structure in response to external perturbations such as harvesting. To identify the mechanisms driving dynamics in the Takvatn system, it was sufficient to have estimates of the relative size distribution (capture per unit effort) of predator and prey, individual growth rates/condition of predator and prey, and estimates of the encounter rate of brown trout with Arctic char (although additional information on the availability of the resource of Arctic char would have been preferable). This information is or could readily be extracted from monitoring data, but that is generally not done at present.

Although we have focused on the basic mechanisms underlying the dynamics of the two systems, both examples have major implications for management. In the Takvatn example, fishing on the prey (Arctic char) of the predator (brown trout) represents a management tool that can promote the recovery of the predator and also reduce the risk of predator collapse (Persson *et al.*, 2007). In cannibalistic systems, size selective harvesting of larger individuals in stable, non-oscillatory systems may induce the production of large "giant" individuals but at the same time induce oscillations as observed for the perch systems (van Kooten *et al.*, 2010).

To conclude, we argue that unless the size-specific interaction strengths between size-structured predator and size-structured prey are explicitly considered, attempts to understand whole-system dynamics will be futile. The extent to which a full quantitative accounting of all individual-level rates in the form of a more detailed DEB model is necessary to understand system dynamics (as was the case for the cannibalistic system) will likely differ between systems and also depend on the extent to which quantitative information is necessary for a particular management purpose. A relevant question to raise here is therefore to what extent existing fisheries management models, especially multispecies models, implement the modelling philosophy embedded in physiologically structured population models with its explicit links between individual-, population-, and community-level processes.

Models for marine fish stocks: ecological considerations

In the current section, we review some commonly used fish stock assessment models with an explicit focus on multispecies models and discuss the question to what extent these models account for (i) size-dependent interactions, (ii) food-dependent somatic growth, and (iii) closed DEB of individuals, which elements were shown above to be crucial for understanding whole-system dynamics. We consequently consider whether these models account for a consistent energy flow in the ecosystem under assessment.

The most prominent objective of collecting fisheries data is to enable predictions of future stock production. Several multispecies models that are commonly used for making such predictions, or seen as front-runners in ecosystem-based approaches to fisheries, are listed in Table 1. In this table, we highlight seven model characteristics that are related to basic processes underlying ecosystem and community dynamics (which per definition pertains to a multispecies context). Specifically, the treatment of the link between intake of food and production of biomass is emphasized. In traditional approaches to model fish stock dynamics, the relationship between age, length, and weight is considered to be constant, which invokes the implicit assumption that individual body condition is also constant, and growth processes are not linked to food availability.

Probably the most used and most well-known multispecies assessment technique is MSVPA (multispecies virtual population analysis, Sparre, 1991). Both MSVPA and the SMS technique (stochastic multispecies model, Lewy and Vinther, 2004) are age-based methods that can account for multiple interacting species. These methods assume fish cohorts to follow a prescribed length–age relationship, which implies that growth is not linked to the availability of resources. Furthermore, the inclusion of predation interactions solely accounts for the (negative) mortality component caused by predation, while its positive effect, the biomass production of the predator population, is independent of the predation interaction and, hence, of prey availability. These models therefore do not capture any of the above listed three ingredients to enable a linkage between individual-level dynamics and population- and community-level dynamics. However, MSGVPA (Gislason, 1999) is an extended version of MSVPA that accounts for dynamic, food-dependent growth, though only for the predator and not for prey species. The stochastic foodweb model as described in Lindegren *et al.* (2009) is specifically designed in the context of an ecosystem-based management approach. Although this model accounts for a relatively extensive foodweb, population size distributions are ignored. With respect to the consistency of energy flows, it may be even more significant that the feeding links, being based on statistical correlations between total population biomasses, are not always reciprocal, meaning that predation mortality may be accounted for without a link to the concomitant food intake of the predator or *vice versa*.

Besides the food-dependence of growth, there is often an energetic inconsistency in the way reproduction or recruitment is accounted for in the models listed in Table 1. The Piscator model (van Nes *et al.*, 2002) goes a long way in accounting for food-dependent growth, but in this framework there is no connection between juvenile recruitment and the fecundity of the spawning

Table 1. Biological properties of some multispecies models used in the context of ecosystem based approaches to fisheries.

Ref	Type	Multispecies	Age	Body size	Food-dependent growth	Length – age relation	Predation effects	Reproduction/recruitment	Closed mass/energy budget
1	MSVPA	+	+	–	–	Fixed	Prey mortality only	Ricker	–
2	MSGVPA	+	+	+	Predator only	Food-dependent (in predator)	Prey mortality only	Ricker	–
3	SMS	+	+	+	–	Fixed	Prey mortality only	e.g. Ricker	–
4	Gadget	+	+	+	–	Dependent on feeding level	Prey mortality and predator feeding level ↑	Fecundity recruitment possible	No direct link between growth and actual food intake
5	Atlantis	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	Size- and condition-dependent spawning	No maintenance costs
6	EwE	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	Condition-dependent	No costs for reproduction
7	Stochastic foodweb model	+	–	–	–	–	Prey mortality and predator biomass ↑	Hydrographically driven	–
8	Piscator	+	+	+	+	Dynamic	Prey mortality and predator food intake ↑	No connection to spawning or spawner condition/abundance	No link between recruitment and spawners

(1) Sparre (1991); (2) Gislason (1999); (3) Lewy and Vinther (2004); (4) Begley and Howell (2004); (5) Fulton *et al.* (2004); (6) Walters *et al.* (2008); (7) Lindegren *et al.* (2009); (8) Van Nes *et al.* (2002).

population. The model frameworks of Gadget, Atlantis, and Ecopath with Ecosim (EwE) in principle link the reproductive output or juvenile recruitment to individual body-size or body-condition and population size distribution. Nevertheless, in these models, the energetic basis of at least one basic process is modelled in a manner that violates mass conservation principles (Table 1).

The formalism of stage-structured biomass models (*sensu* De Roos *et al.*, 2008) shows similarities with the approach adopted in EwE (Walters *et al.*, 2008; Table 1), in particular in terms of "user friendliness" and simplicity of equations. The two formalisms nevertheless differ in the way energy flows are modelled, especially with respect to maturation (biomass flow into subsequent life stages) and reproduction (biomass flow from adults to newborn individuals). In the EwE framework, maturation can in principle be represented as a food-dependent flow, but there is no published example exploiting that possibility in the context of a multispecies model and usually maturation is modelled as a constant process (Christensen and Walters, 2004). In addition, the EwE framework generally does not account for biomass costs of reproduction, which in essence allows for a spontaneous source of newborn biomass. The stage-structure biomass formulation, in contrast, models individual-level energetics with a closed DEB model, which makes maturation and reproduction rate dependent upon food intake and thus closes the loop of energy in- and outflow to the system (Table 1).

On the basis of the seven model characteristics highlighted in Table 1, we conclude that none of the models commonly used for fish stock assessment, management advice, or as a conceptual model considering ecosystem dynamics for an ecosystem-based approach to fisheries (e.g. Plagányi, 2007) bases itself on a completely closed mass/energy budget and that these models thus violate the basic law of conservation of mass/energy. Such a lack of a complete handling of mass balances is not a trivial problem as illustrated by the cannibalistic perch system where a quantitatively correct handling of mass flows was pivotal for understanding overall system dynamics.

Linking individuals to populations and communities: insights from monitoring data

Utilizing the Takvatn example, we test the hypothesis that a relatively limited amount of information can be sufficient to unravel the underlying processes that may cause major changes in community structure as a response to external perturbations such as harvesting. We use existing stock assessment data of two marine fish species, the predatory cod (*Gadus morhua*) and one of its main prey fish sprat (*Sprattus sprattus*) (the other being herring, *Clupea harengus*) in the Baltic Sea system, in combination with data available on zooplankton to look for relationships between resource or prey density and consumer (sprat and cod) growth performance. The question we address is whether the collected data are sufficient to obtain information about (i) size-specific interactions between individuals; (ii) food-dependent growth; and (iii) food-dependent reproduction.

Besides being the most abundant fish species, the populations of cod and sprat in the Baltic Sea are commercially important stocks and have been industrially fished with increasing intensity since the 1960s. Although since the 1970s stock assessments have been made and used for advice on fishing intensity, a steep decline and collapse of the cod stocks in the early 1990s could not be prevented nor reverted by the commonly adopted methods. The collapse of the cod stock resulted in a shift visible at four trophic levels in the ecosystem (Casini *et al.*, 2008; Möllmann *et al.*, 2008). The occurrence of, and need to understand, such ecosystem-wide events calls forth an ecological perspective when considering the population dynamics of commercially important marine stocks.

Previous analyses of the Baltic cod and sprat populations showed the distinction between two periods, one with dominance of the predator cod (i.e. the period <1994) and a second period with dominance of the zooplanktivore sprat (≥1994), which followed the overfishing of the cod stock (Casini *et al.*, 2008). Furthermore, in the second period, the abundance of sprat individuals (age 1+) is positively correlated with the biomass of the zooplankton resource base, a relation lacking in the first period (Casini *et al.*, 2008). A plot of the seasonal growth of individual sprat as a function of the resource (zooplankton) biomass shows the same outcome, with individual sprat growth being positively correlated with the resource availability only in the second period, in which the cod population is at a low biomass, (Figure 5b). In contrast, no relationship is present in the period with dominance of the top predator (Figure 5a).

The population data of sprat and its zooplankton prey thus provide evidence for energy-dependent growth in the period when the system is dominated by bottom-up control, whereas the relationship is absent in the period when top-down processes play a more important role. Since the first period is characterized by top-down control of the sprat population, the zooplankton densities would be predicted to be higher, relative to a bottom-up controlled situation. Comparison of the two panels in Figure 5, however, shows that there is a large overlap in the measured densities of zooplankton. Moreover, even the realized growth of sprat has comparable levels between the two periods, which contrasts with expectations under top-down vs. bottom-up scenarios.

The occurrence of these patterns (and their absence), both highlights the potential of the data, as well as shows its limitations. Logically, there must be a connection between individual growth and availability of resources. The representation of resource density by a single data point each year is apparently sufficient to reveal a connection in the variation of individual growth and food availability for the zooplanktivore sprat, as long as the dynamics are regulated by bottom-up control. On the other hand, the same data resolution, in time, but specifically in terms of prey sizes, is insufficient to reveal the relation of body size growth in cod with availability of its food. To investigate the relationship between individual cod growth and the density of its major fish prey, we used the yearly total sprat biomass estimated in autumn. The growth data for cod are based on cohort estimates of yearly increments in average weight for cohorts with ages 3+ years old (>30 cm). Acoustic data for sprat, including average weight-at-age for different cohorts contains data for ages 1-year old and older (>8 cm). Sprat individuals in these cohorts all fall within the predation window of cod aged 3+ and because the relative component of alternative resources in the cod diet is unknown, we take the total sprat biomass as an indicator of available food for cod. The analysis shows that there is no relation between individual cod growth and the total biomass of its major prey species, in neither of the two periods (Figure 6). With respect to the energy dependence of biomass increase in cod cohorts, the population-level indicator of prey availability does therefore not confer the essential components for realized predator growth. This result is not *per se* surprising, when viewed in light of the patterns found between predator and prey fish in the Takvatn system (Figure 1), but again points to the need for prey fish data with a high size resolution.

Besides the size- and time-resolution issue with respect to the data of the resource base of cod, it is problematic that the resource is represented as a single unit (sprat population biomass): cod is known to additionally forage upon herring, benthic macroinvertebrates, and zooplankton, but it is not known how important (in terms of energy dependence) these different prey are for cod of different sizes. The lack of this knowledge renders it impossible to use the data presented in Figure 6 for a derivation of empirical consumption rate of sprat by cod. The origin of this issue is impossible to solve by only collecting better data and can therefore be considered of a more basic nature than the issue of time and size resolution

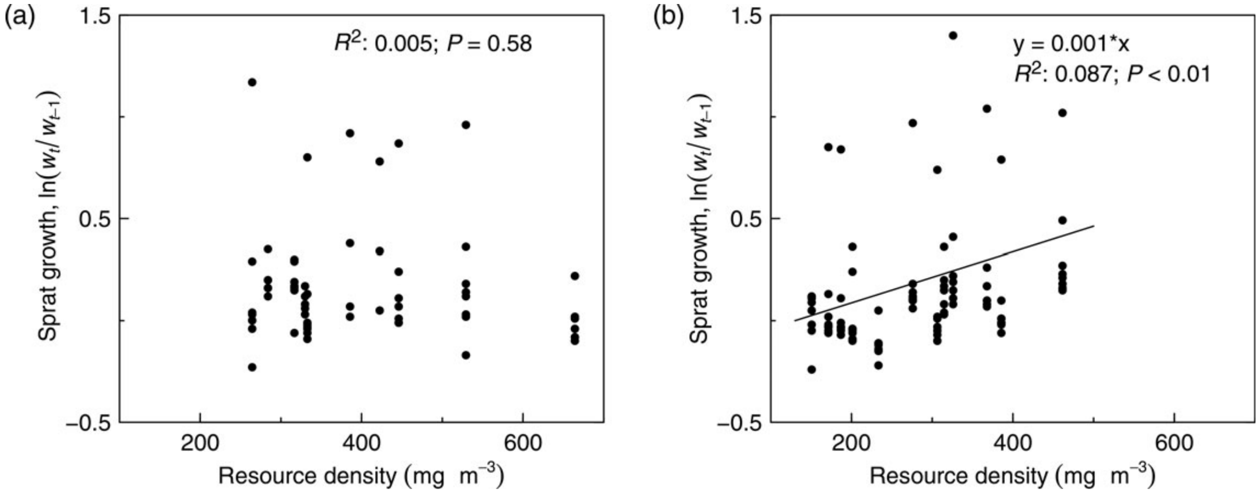

Figure 5. Annual increase in average weight in the Baltic sprat population (age 1+, 1978 – 2007) as a function of zooplankton density. (a) Sprat growth in the years where the sprat population is below the threshold level (1978 – 1994, as established in Casini *et al.*, 2009), sprat growth is derived from weight-at-age data from the acoustic survey in SD28 (carried out by Sweden and Latvia), Baltic Sea, resource density represents the summer density of zooplankton (sum of *Acartia*, *Pseudocalanus*, *Temora*, *and Cladoceran* species; all unpublished data, Michele Casini, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Lysekil). (b) Sprat growth in the period 1994 – 2007, the period in which the sprat population density was above the threshold level and regulated by bottom-up control (Casini *et al.*, 2009).

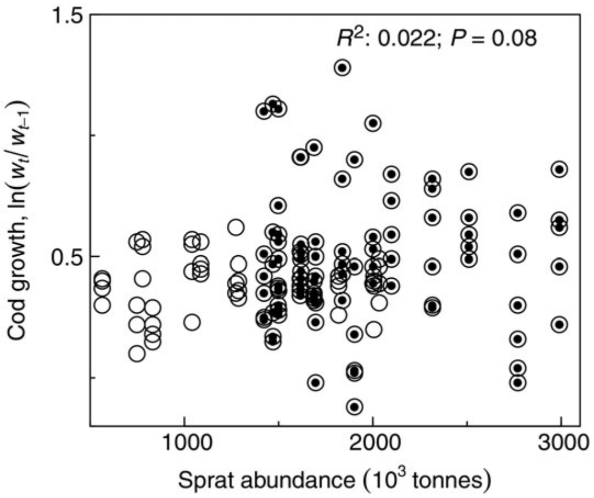

Figure 6. Annual increase in average weight in the Baltic Sea cod population (age 3+, 1982–2010) as a function of sprat total biomass (age 1+, all data from ICES, WGBFAS2011 – ACOM:10, Table 2.4.13; Table 7.7). Cod weight-at-age data in years <1982 was left out because preceding this date a constant weight-at-age is assumed in the stock assessment data. The dots with a thick dot inserted indicate the data for the years the sprat population density was above the threshold level and regulated by bottom-up control (Casini *et al.*, 2009).

in the data. The measured effect shown in these data (average weight increase in age cohorts) is a result of several processes, taking place at the individual level. Yearly individual growth is the outcome of food intake and energy expenditure over the course of the preceding growth season. Furthermore, food intake in cod depends on the availability and densities of the different prey listed above; energy expenditure depends on activity, baseline metabolism, and allocation to reproductive tissue. To take just one measure (weight increase) as a representation of these many variables is taking a short-cut, preventing a clear view on those variables themselves. Inference of individual growth potential from such observations at the system level is virtually infeasible. At the same time, the inference of the essential community structure (trophic configuration) from individual-level observations (such as stomach data) can also be misleading. As illustrated by the cannibalistic perch example mortality by cannibalism may be substantial and to a large extent shape community dynamics (in the stunted phases of the dynamics), while the diet of the cannibals mainly consists of macroinvertebrate prey (cf. Figure 4a and b). Therefore, the diet of individuals can be analysed in the field, but it should be kept in mind that diets represent the output of the feeding process and can hence not serve as input to parameterize this process in a model that accounts for a mechanistic (bottom-up) system description. Furthermore, the mere occurrence of a feeding interaction (e.g. macrobenthos feeding by cannibalistic perch) does not imply that this interaction actually plays a major role in determining community dynamics (Persson *et al.*, 2007, 2013; Persson and De Roos, 2012).

Discussion

Overall, we have discussed three major interrelated issues: the problem of deducing an appropriate trophic configuration based on which to analyse a system; the necessity to mechanistically link individual, population, and community processes to obtain an understanding of whole-system dynamics; and the issue of accounting for closed energy budgets and mass conservation and the extent to which this is done in contemporary multispecies fisheries models.

Trophic structure and niche shifts

Deducing an appropriate trophic configuration for the system to be studied is not a trivial task. As pointed out above, the use of observed diet data can be problematic, since the observed diet represents the result of interactions and cannot be taken directly to reflect the underlying processes. The individual diet, as it is observed, results as an output from size-dependent feeding interactions and encounter or availability of different prey and resources, which are the true input. Many observed feeding relationships may furthermore be unimportant in explaining community dynamics and structure (Persson and De Roos, 2012; Persson *et al.*, 2013), however, frequently occurring. It may even be so that a low incidence of prey fish in the diet of predators represents a high predation impact on the prey fish, or *vice versa*, as was the case in the cannibalistic perch system.

In view of the ecosystem changes happening worldwide in diverse systems, which are sometimes caused by anthropogenic impacts, we argue that despite its difficulties, building an understanding of trophic interconnections and foodweb structure is an essential component for an ecosystem-based assessment and management of fisheries. We propose that a number of steps can be taken to move forward, the first of which deals with the form of ontogenetic niche shifts that occur with increasing fish size. These shifts can be gradual and involve an addition of larger prey sizes where the smallest prey sizes stay more or less the same, or they may be discrete where smaller prey items are dropped from the diet when larger prey items are included (Werner and Gilliam, 1984; Schellekens *et al.*, 2010). Modelling of size-structured systems has shown that the shape of the ontogenetic niche shifts in predator life history and particularly whether the predator can mature on non-piscivorous resources has a major effect on community structure (Van de Wolfshaar *et al.*, 2006; Hin *et al.*, 2011; De Roos and Persson, 2013; van Leeuwen *et al.*, 2013). To unravel this ecological aspect of the life history of the predator species represents the first important step to reach an appropriate characterization of the trophic structure (cf. Huss *et al.*, 2013). Second, the extent to which top-down effects can occur when top predators experience multiple (zooplanktivory–benthivory–piscivory) niche shifts during life may depend heavily on the discreteness of their ontogenetic niche shifts (Van de Wolfshaar *et al.*, 2006; van Leeuwen *et al.*, 2013). Existing theory and empirical studies here suggest that it may be possible to use observed individual-level growth trajectories in combination with size-distributed densities of interacting fish populations (preferably also resource levels) to track dynamically important interactions, because patterns in these data can distinguish between different trophic configurations (Persson *et al.*, 2003, 2007; Van de Wolfshaar *et al.*, 2006; De Roos and Persson, 2013; van Leeuwen *et al.*, 2013). For example, for the Baltic Sea system, three major mechanisms have been proposed to potentially explain the changes in the fish community: an Emergent Allee effect as in the Takvatn system, mixed competition/predation interactions (or cultivation/depensation) between predatory fish and prey fish and predation on early life stages of the top predator cod by prey fish (van Leeuwen *et al.*, 2013). Modelling studies show that these three scenarios yield vastly different individual growth curves of the top predator and also different size distributions of predator and prey fish (De Roos and Persson, 2013). The attempt to resolve which of these three processes contributes most to explaining the dynamics of the Baltic system should thus be based on empirical analyses of patterns at the population (e.g. size distributions) and individual (cf. individual growth rates of predator and prey) levels.

Individual to population to community

Our analysis of the perch–zooplankton interactions in Abborrtjärn 3 and partly also the sprat–zooplankton interactions in the Baltic Sea suggests that a relationship (although poor) between resource level and individual planktivorous consumer performance can be present even when resource availability is represented by a single point estimate in terms of total resource biomass (for the strength of the interaction the size of the consumer must still be taken into consideration). This may be a result of the limited size variation in the resource and the average size of resource compared with the consumer being relatively small. In contrast, fish predator–prey interactions are characterized by major changes in size of both prey fish and predator fish, and in this case, a condensed biomass estimate in terms of total biomass will inevitably fail in allowing an establishment of a relationship between prey availability and individual performance. Even worse, the Takvatn example shows that there may actually be a negative relationship between total prey fish biomass and predator performance. To appropriately characterize these interactions, it is therefore basic to incorporate size-dependent interactions between predator and prey.

One of the major advantages of the physiologically structured population models that we used in our freshwater examples is that they allow for a more critical testing of model predictions, involving both population-level information such as population size distributions and individual-level information such as individual growth curves that are shaped by ecological feedbacks (Figures 1, 3, and 4). It is worthy to note that fisheries sampling programs often include information at both these levels of organization. Although the data collection procedure may be limiting, data on population abundances and size distributions as well as growth curves are often present, but generally not used efficiently in an integrated way to investigate population and community dynamics. The dynamics of the Takvatn system that we discussed extensively in the text above illustrate the kind of analyses that can be carried out with an actually limited amount of information (Figure 1). At the same time, it is obvious that more complete analyses of the dynamics of this system could have been done if information had also been available on (zooplankton and macroinvertebrate) resource levels and the seasonal abundance of the smallest size classes of Arctic char (<80 mm). Having access to and efficiently using time-series data on predatory fish and prey with a high intraspecific size resolution, individual growth curves and resource levels will undoubtedly form the basis for a true ecosystem-based management approach that takes into account relevant ecological feedbacks.

The two freshwater examples we have used undoubtedly represent rather simple systems in terms of the number of fish species involved. Still, the framework we propose has been used to understand the dynamics of, for example, the multispecies fish community of Lake Victoria (Downing *et al.*, 2013). This suggests that the dynamics of species-rich fish systems may be possible to assess with a relatively limited amount of information. The changes in the ecological system in Lake Victoria are still driven by the dynamics of one dominant top predator, the Nile perch (Goudswaard *et al.*, 2008). To obtain robust tools for both assessment and management of systems with many top predatory fish species undergoing multiple ontogenetic niche shifts represent a major challenge for future research.

Accounting for energy budgets and mass conservation

For fish, as for all living organisms, growth and reproduction (i.e. the production of biomass) come at an energy cost. Availability of this energy depends on food intake. To ignore food-dependent development in projections of (population) biomass production equals implicitly assuming a "free" energy source to the system. Essentially, whether or not to enforce strict mass conservation boils down to a modelling philosophy decision between on the one hand a specification of whole-system dynamics in terms of the underlying, mechanistic processes at the individual level or, alternatively, a mimicking of these dynamics by combining observed, but not necessarily causal, relations into a phenomenological system description. However detailed, the latter will by its nature be less likely to correctly extrapolate system dynamics to novel environmental conditions. We have particularly considered the incorporation of food-dependent growth and a coupling between energy intake and reproductive output (including a cost for reproduction) in existing models used for fish stock assessments and stock predictions. The overview given in Table 1 shows that none of these models are based on a fully consistent incorporation of the individual-level processes and energy conservation. Ignoring the food-dependent basis of both development and reproductive output completely could be justified when there would be no or only limited effects of doing this. Our two examples from freshwater systems show that food-dependent growth and reproduction are both vital processes affecting population and community dynamics. The extent to which a complete handling of mass balances as for the perch system is important will likely differ between systems and also depend on the questions addressed, but should be increasingly important when questions related to harvesting yields are decided. Quantitative predictions may also become more important when effects of environmental variation such as temperature variation are included because changes in temperature, for example, affects both individual-level processes (intake an metabolism) and community-level processes (e.g. resource productivity) where the dynamical outcome depends on the relative scaling of these processes (Vasseur and McCann, 2005).

A possible reason for the lack of a consistent link between energy intake and allocation to reproductive output and recruitment in several fisheries models may be a disagreement about the role, the extent and the mechanisms of larval mortality (e.g. Hjort's 1914 "critical larval period" concept; Elliott, 1989; Jenkins *et al.*, 1991; Houde, 1994, 1997; Persson *et al.*, 2000b) which partly explains the commonly observed high, unexplained variation in stock–recruitment curves. These factors may have led fisheries scientists to conclude that there is little meaning in making reproductive output depend on the energetic state of the reproducing individuals and instead assume it to be stochastic or dependent on environmental factors only. One problem here is that recruitment of a cohort generally refers to a cohort at an age (or size) when major density-dependent interactions have already taken place. Considering the major change in size that a fish individual undergoes during its first growing season, an understanding of the community dynamics may critically depend on a sufficient resolution in size and thereby also time resolution, which current stock–recruitment models do not capture.

As discussed here, the approaches to management of fisheries and fish stocks has so far neglected essential ecology of fish and fish population dynamics. The ecosystem-based management approach to fisheries management is supposed to take into account the ecological consequences of fisheries for entire ecosystems. We have shown that an understanding of population dynamics, which is based on mechanistic descriptions of individual-level processes, can reveal the way and processes by which populations are regulated. Changes in stock size distributions and variation in individual body sizes of age cohorts represent invaluable data of commercial fish stocks in this regard, which was already clearly recognized since the days of Hjort (1914). Creating a connection between such data and the underlying ecological foundation of that variation is the necessary and vital next step towards an understanding of the ecosystem wide impacts regarding system structure and dynamics as a result from imposing fishing pressure and other perturbations. Doing this is the way forward in pursuit of a true ecosystem-based approach to fisheries.

Supplementary material

Supplementary material includes the ecological background to and derivation of the functions used for calculating encounter rate for brown trout with Arctic char and cannibalistic perch with perch victims.

Acknowledgements

The research based on which this paper was written was supported by grants from the Dutch Science foundation to André De Roos, from the Swedish Research Council to Lennart Persson, and from the Swedish Environmental Protection Agency and the Swedish Board of Fisheries to Anieke van Leeuwen. We also thank three anonymous reviewers for very useful comments on the manuscript.

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Handling editor: Marta Coll

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2281–2292. doi:10.1093/icesjms/fst242

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food for Thought

Active opportunist species as potential diagnostic markers for comparative tracking of complex marine ecosystem responses to global trends

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Bakun, A. Active opportunist species as potential diagnostic markers for comparative tracking of complex marine ecosystem responses to global trends. – ICES Journal of Marine Science, 71: 2281–2292.

Received 9 December 2013; accepted 26 December 2013; advance access publication 7 February 2014

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As it becomes ever clearer that on longer time scales marine ecosystems function as non-linear "complex adaptive systems", potential consequences of global change become obscured within a maze of multiple possibilities. This essay attempts to route one pathway to a potentially more robust conceptual synthesis, employing the globally important example of anchovies and sardines as a model. Expressly, the anchovy emerges as an efficient specialist of neritic origin. In contrast, the sardine's oceanic-based adaptations equip it to deal with intermittent episodes of poorly productive conditions and to take advantage of associated reduction in predation pressure on early life stages of their offspring. Based on the overall synthesis, the nimble, wide-ranging, actively opportunistic sardine appears notably well equipped to deal with climate-related disruptions and dislocations and even to profit from their adverse effects on predators and competitors. Global-scale multispecies population synchronies in the 1970s to the mid-1980s suggest that a variety of different species types might be flagged for investigation as perhaps embodying similar "active opportunist" attributes. If so, events and anecdotes might, as global changes proceed, be viewed within a developing universal framework that could support increasingly effective transfers of experience and predictive foresight across different species groups and regional ecosystems.

Keywords: climate change, earth systems models, global climate models, representative concentration pathways.

Introduction

In the century that has passed since Johan Hjort's (1914) seminal publication, much has been learned about the intricate linkages of physical and biological mechanisms operating within the structures of marine ecosystems. Even so, there has been precious little success in applying that progress towards improving fisheries management and marine conservation efforts, i.e. towards the "ultimate"-level goals of long-term preservation of the traditional economic and esthetic benefits that have come to be expected to flow forth from the world's marine ecosystems. Perplexingly, our current understanding of the dynamics of these systems remains rife with puzzles and paradoxes (e.g. Bakun, 2011, 2012), and actionably reliable prediction continues to evade us (Houde, 2008). This is much in contrast to many other fields of modern science in which the spread of successful applications has been explosive.

Certainly, part of the problem must be that we humans are not marine organisms, but are terrestrial ones. Our experiences, as well as our intuitions, are overwhelmingly terrestrially based. Not surprisingly, our conventional conceptual frameworks for understanding how marine ecosystem processes may influence population dynamics are, both at Hjort's time and at present, rather simple reflections of terrestrial analogies. But the "marine world" is something qualitatively different and in many ways "beyond our human experience" (Bakun, 1996). For example, in terms of such references as numbers of trophic levels or varieties of dynamical feedbacks involved, marine systems are in nearly all cases much the more complex.

Moreover, as historical data records have lengthened, it has become ever more evident that on longer time scales, marine ecosystems seem to be functioning as classical complex adaptive systems (Levin, 1998, 1999), characterized by dynamical non-linearities

(Hsieh *et al.*, 2005) and self-enhancing feedback loops (Bakun and Weeks, 2006). Dynamical systems of this type tend towards chaotic, non-predictable behaviour, calling into question the very efficacy of scientific management efforts. In particular, since non-linear mathematics do not necessarily yield unique solutions, potential consequences of various aspects of global change tend to become diffused in a nebulous array of multiple possibilities. Certainly, once it is realized that conventional assumptions of system stationarity are becoming increasingly untenable, the sorts of simple linear models (e.g. fitting of indices of reproductive success to one or several indices of correlated environmental or ecosystem mechanisms) that have become traditional in fisheries science, lose their credibility as reliable harbingers of the future. Fortunately, such a pessimistic perspective is contradicted by certain striking regularities and temporal-spatial correspondences that seem to evoke a more promising viewpoint. Among the most remarkable of these have involved interactions between the anchovy (genus *Engraulis*) and sardine (genera *Sardinops* and *Sardina*) species groups.

Anchovies and sardines coexist at the crucial wasp-waist position (Rice, 1995; Bakun, 1996, 2006a; Cury *et al.*, 2000) in the trophic structures of a surprising variety of important regional marine ecosystems. Their populations tend to be large, often comprising the greater part of the entire animal biomass of the local ecosystem in which they function. Therefore, they tend to support quite massive fisheries, such that variations in production from the anchovy–sardine pair have often been dominant factors in the overall variability in world fish production. In turn, the very efficient and powerful fisheries focused on these stocks exert important controls on their population dynamics.

Notably, the two species groups have historically exhibited a tendency to alternate in ascendancy at the wasp waist of a given regional ecosystem on time scales of several years to several decades, generating differing ecosystem effects depending on which may be dominant at a particular time. For example, anchovies are largely zooplanktivores, whereas sardines are more omnivorous in that they have greater capability to effectively consume phytoplankton as well as zooplankton. Thus, anchovy dominance may promote higher ratios of phytoplankton to zooplankton (Cury *et al.*, 2000), perhaps therefore favouring eutrophication and associated hypoxia. On the other hand, since herbivorous zooplankton may preferentially consume diatoms over dinoflagelates, the higher ratios of zooplankton that may be associated with sardine dominance may favour toxic "red tide" dinoflagelate blooms (Irigoien *et al.*, 2005). Moreover, sardines tend to spread their operations over much wider ocean areas, whereas anchovies tend to remain concentrated in more restricted home-range zones. Thus, a change in dominance between the two has important consequences with respect to many aspects of geographic patterning of marine ecosystem processes.

Puzzling issues with respect to the interactions of this pair of species groups include the following (Bakun and Broad, 2003).

(A) The fact that sardines, which are a species group obviously adapted to highly productive ocean conditions (upwelling areas, etc.), often do better, at least in the eastern Pacific, during *El Niño* episodes—which paradoxically are characterized by abruptly lowered primary productivity.

(B) The extraordinary fish productivity of the Peru–Humboldt large marine ecosystem (LME), which largely rests on the productivity of the anchovy–sardine species pair.

(C) A pervasive tendency for out-of-phase population oscillations leading to alternating dominance of anchovies and sardines in any given regional ecosystem.

(D) Basin-scale synchronies in sardine population expansions and contractions during the 1970s and the 1980s—although the involved populations exist in very different types of ecosystems, which accordingly could be expected to respond quite differently to the same large-scale forcing characteristics.

An additional unexplained issue (which can here be labelled "E") involves the fact that these two species types manage to cohabit a remarkable number of diversely configured regional-scale marine ecosystems, in apparent contradiction of the competitive exclusion principle (Hardin, 1960).

Although it is difficult to rejoice over the existence of conspicuous gaps in our understanding, prominent existing paradoxical issues such as these do represent remarkable opportunities to hone directly in on essential mechanisms and thereby avoid becoming lost in irrelevant details and distractions. The wealth of such "conundrums" represented in the list above (issues A though E) provides an essential inferential basis that underlies the conclusions and generalizations presented here.

In the many years that fisheries scientists have been puzzling over these and other seemingly paradoxical patterns of correspondence and evident interaction, quite a collection of proposed hypotheses as well as *ad hoc* explanations have been amassed. At the point they are proposed, these generally provide a reasonable degree of empirical fit to the past data that largely motivated them. However, the degree of fit seldom holds up through subsequent years. A basic problem is that the standard experimental method is clearly not practical on the scales at which the earth's coupled ocean–atmosphere system and its entrained marine biological processes interact to regulate dynamics of wide-ranging, mobile marine populations. Moreover, the rises and declines in dominant fishery resource stocks tend to play out over decadal or multidecadal time scales, whereas most available *in situ* dataseries, as well as acceptably homogeneous fisheries catch dataseries, do not exceed a few decades in length. As a result, the number of actual realizations of such major changes available in any real dataseries tends to be too small in any single regional case to empirically sort out the complexity of interactions among the various driving factors and non-stationary linkage mechanisms. Although constructing computer-driven simulation models to explore and demonstrate the outcomes of combining particular sets of mechanisms and processes is currently a very popular activity, such simulations can of course only reflect the knowledge and assumptions that were put into them; they cannot generate independent new data.

Some alleviation of the insufficiency in empirical degrees of freedom may be sought via an interregional comparative approach. This requires a willingness to accept that parallel aspects of essential processes and relationships controlling the dynamics and interrelationships of highly similar species groups should operate in a generally analogous manner, after allowing for regional particulars, in different available regional situations. If this willingness exists, the comparative method (Mayr, 1982) opens the door to considerably augmented inferential power, although suitable analysis procedures may not necessarily be simple or straightforward. Generally, if a coherent hypothetical formulation should be found to be capable of explaining a number of paradoxical, or otherwise remarkable, observed patterns, scientific confidence expands. If it appears uniquely so (i.e. no other explanatory basis is found that can withstand serious examination), one may reasonably decide, at least tentatively, to place reliance on it.

MacCall (2009a) listed a number of candidate mechanisms that may underlie anchovy–sardine interactions, most of which seem likely to be involved to greater or lesser degree at various times. For even more potential explanatory "ingredients", one might refer to several of the chapters in the "Berlin Workshop" volume of Journal of Marine Systems (Alheit *et al.*, 2009), and a succession of other symposium volumes and workshop reports stretching back to the pivotal "Lima Workshop" (Sharp, 1980). But here we first try to gain some independent discriminatory power to help navigate the labyrinth of proposed hypotheses and mechanisms. We do so by standing back a bit from the details and widening the focus to encompass a more general view of the two species groups in terms of what might be directly inferred from their apparent evolution, genetic characteristics, adaptations, and evolved capabilities.

Certainly, the manifested comparative patterns ("A" though "E", listed above) are so striking that the idea that they might spontaneously materialize from some variable mix of largely autonomous mechanisms strains credulity. Rather, a satisfying explanation would seem to require some overall organizing principle, basic to all the otherwise puzzling issues listed above, that could somehow weave together the outcomes of multiple active component mechanisms so as to logically lead to the pervasive patterns that are observed.

Differing evolutions and adaptations

To try to initiate a comparative inferential search at the most basic evolutionary level possible, it may be useful to begin by considering the differing developmental origins of the respective anchovy and sardine species groups. (The discussion that follows in this section is summarized diagrammatically in Figure 1.)

Anchovies

In gross aspect, the evolution of the anchovy (genus *Engraulis*) would seem to have had its primary basis in terrestrially conditioned habitats (river plume environments, estuaries, run-off-influenced semi-enclosed seas and bays, broad sedimentary continental shelves, etc.). For example, because of the westward tectonic movement of the American continents, high mountain barriers and narrow continental shelves characterize their western continental boundaries. As a result, the overwhelming portion of continental run-off flows to their Atlantic Ocean sides, which (being the "trailing" continental edge with respect to tectonic plate movement) tend to feature much broader continental shelves and very extensive shallow estuarine systems. Substantial anchovy (*Engraulis*) populations exist all along the temperate western Atlantic ocean boundary, with one of the largest anchovy populations of the world (*E. anchoita*) stretching along an enormous stretch of very broad South American continental shelf. In contrast, temperate sardines (*Sardinops* or *Sardina*) are entirely absent from the western side of the Atlantic. The pattern of association of anchovies with river plume/estuarine/terrestrial-conditioned environments continues to hold also on somewhat smaller scales—for example, among the intricately patterned Mediterranean Sea environments (Palomera and Rubies, 1996) and also recently within the North and Baltic Seas (Alheit *et al.*, 2012).

A revealing example comes from the Gulf of California, where one of the great rivers of North America, the Colorado, used to flow copiously into its upper (northern) end. That inflow has steadily vanished over the past century as a result of steadily increasing impoundment to supply agricultural irrigation for much of the southwestern United States. In the memory of fishers operating there in the latter 20th century, an anchovy had never been seen in the Gulf before 1986 (Hammann and Cisneros-Mata, 1989), when anchovies briefly appeared following an abrupt collapse of the local sardine resource. Later, a subsequent analysis of fish scale deposits in anaerobic sea floor sediments (Holmgren-Urba and Baumgartner, 1993) indicated that this was not the first time that anchovies had made an incursion into the Gulf of California, but in fact they had entirely dominated the fish biomass in the Gulf for most of the 19th century. This was when (and here is the illustrative point) the Colorado River was still pouring into the Gulf a major portion of the continental run-off from the great mountain ranges and high plateaus of the southwestern United States.

The higher degree of affinity of anchovies for estuarine-affected habitats is clearly reflected in the much coarser gillraker structures that they employ as food gathering apparatus. As a result, they are incapable of filtering as small a size of food particles as sardines can (van der Lingen, 1994; van der Lingen *et al.*, 2006). But anchovies may thus be able to suffer less clogging of these structures with terrestrial sediment material and other particulate matter that typifies run-off-influenced situations (unblocked flow of water through gill structures being essential also to respiration, an even more immediate need than food gathering). But crucially, precisely because of their coarsely meshed gillrakers, anchovies can efficiently deploy a comparatively much larger "filter basket" (reflected in their local common name often being some variation on "big mouth"). Therefore, anchovies are particularly efficient at gathering large food particles when such particles are plentiful (as they would tend to be in the run-off-dominated terrestrially conditioned near-coastal or estuarine situations in which the genus appears to have primarily evolved). In accordance with this seeming affinity for terrestrial-conditioned environments, the anchovy seems to be quite local in its movements, exhibiting a tendency to both feed and reproduce within restricted, comparatively fixed geographical contexts (river plume edges, local coastal embayments, island complexes, etc.). Thus, the anchovy has evolved to be a relatively weak swimmer and migrator. In any case, their coarse filters would seem to make wide-ranging exploratory activity a risky proposition, in that once an anchovy may wander away from the geographically fixed locations where the larger food particles that it can efficiently gather may be reliably available, it runs serious risk of dangerous problems in gathering adequate food to sustain itself until it encounters the next suitable large-particle "oasis".

Thus, one might surmise that an anchovy would tend to be, in the terminology of Cury (1994), more "obstinate" than "opportunistic" in its migrational tendencies. An associated propensity for local population segmentation is confirmed by the anchovy's comparatively much greater level of genetic diversity (Hedgecock *et al.*, 1989; Grant and Leslie, 1996). The implication is that anchovies expend less of their acquired trophic energy in swimming and migrating than do sardines. Therefore, there is less need for the hydrodynamic advantages associated with larger size, and so the anchovy can afford to mature earlier and at a smaller size, in the process allotting a lesser portion of acquired energy to growth and a greater portion to reproduction and rapid population responses (Figure 1). Because predation in these highly productive shallow, near-coastal zones would be expected to be intense on all life stages, such energetic efficiency and rapidity of population response may be an absolute requirement for long-term population viability.

The "anomaly" to this pattern presented by the remarkable success of the anchovy in the open ocean realm off Peru has been

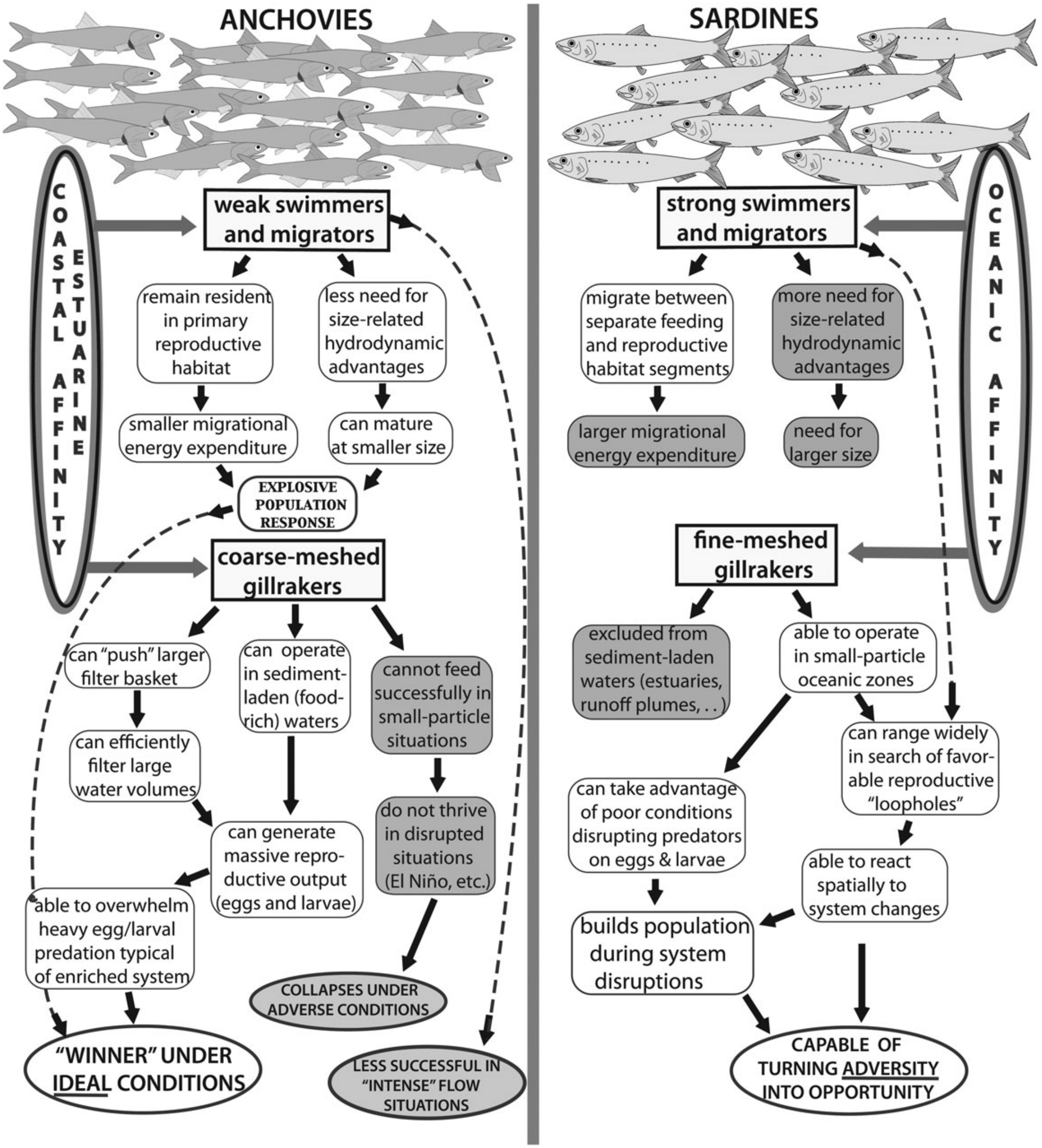

Figure 1. Summary diagram representing the adaptive sequences leading from evident "primary ecological origins" to produce the relative ecological advantages (unshaded text boxes) or disadvantages (shaded text boxes) exhibited by the respective anchovy and sardine species groups.

attributed (Bakun and Weeks, 2008) partially to the special conditions of that very low latitude location which, because of the weakened coriolis effect, presents a particularly benign habitat that is characterized by strong enrichment, weak turbulent mixing, and long particle residence times. Except during *El Niño* situations when nutrient supply is disrupted, these attributes generate particularly dense accumulations of very large chain-forming diatoms and associated larger herbivorous zooplankton species. Thus, the normal Peruvian situation may present analogies to the comparatively turbid, large-particle conditions found in other more terrestrially conditioned anchovy habitats. On the other hand, during an *El Niño* episode, when the available particle spectrum characteristically shifts to a much smaller size range, the Peruvian anchoveta would seem to face quite a direct analogue to the feeding problems that might be faced by a "wandering anchovy" that attempts to transit between dispersed terrestrially determined habitats.

Sardines

Sardines, in contrast, tend to avoid turbid water situations. In particular, they appear to thrive where continental shelves may be narrow, in upwelling systems, and in the edge zones of strong oceanic boundary currents. They appear adept at opportunistically exploiting the benefits of energetically forced eddy fields and of a variety of transient, sporadically distributed convergent frontal situations that develop in more offshore oceanic waters. They are strong swimmers and, particularly for *Sardinops*, prodigiously wide-ranging migrators as befits their relative affinity to the less robustly patterned, more variably configured oceanic realm (i.e. the offshore frontal boundaries where upwelling-conditioned waters or continental shelf waters meet with oceanic waters, or within the favourable segments formed within the energetic eddy fields driven by lateral frictional interactions with strong oceanic boundary current flows). Here, substantial concentrations of food particles large enough to be efficiently gathered by anchovies tend to be relatively rare, and patches even of much smaller potential food particles are patchy, transitory, and more or less ephemeral. In such a case, exploration, innovation, and even a degree of "risky" capriciousness may be advantageous to sardines on an individual basis, while also yielding as a by-product diffused overall risk to the population as a whole.

Moreover, in this less productive offshore zone, predation pressure would be relatively relaxed, except in zones of dynamic concentration such as convergent fronts or convergent eddy segments that may be vital to their reproductive success. But here the sardines' highly mobile, exploratory tendencies may allow them to "get there first", and then "get out" (or at least "do their reproductive business") before larger pelagic predators also locating the zones (e.g. guided by the presence of flotsam and drifting objects that would begin to progressively accumulate rather immediately after the particular convergence zones develop) and arriving *en masse* to truncate the transient local advantage that the sardines may have initially enjoyed.

At the population level, sardines are strikingly proficient at opportunistically expanding or altering the geographical locations and extents of their spheres of operation (Lluch-Belda *et al.*, 1989; Kuroda, 1991). Their geographical gyrations are matched by radical abundance variations, suggestive of a "high-risk" opportunistic life strategy that seeks to initially overwhelm and then outmanoeuvre adverse ecological pressures by relentlessly ferreting out opportune "loopholes" (Bakun and Broad, 2003) in the ambient predation pressures wherever they might exist.

This impression of wide-ranging, "high-risk" operation by the sardine is bolstered by genetic data (Lecomte *et al.*, 2004) that, for example, indicates quite a recent sardine history in the northeast Pacific (a quarter million years) compared with the anchovy's (5 million years). Such a comparatively recent "founder event" has also been supported by allozyme data, which indicated reduced levels of diversity relative to anchovies and other clupeoids (Hedgecock *et al.*, 1989; Grant and Leslie, 1996). This degree of shallowness in genetic divergences among regional populations may be explained by two alternative models of population persistence and dispersal (Grant and Bowen, 1998). Either (1) *Sardinops* may have inhabited a limited area for most of the last 20 million years before expanding to the temperate corners of the Indian and Pacific regions in the last few hundred thousand years or (2) the various regional *Sardinops* populations may have been extinguished repeatedly and subsequently recolonized by opportunistic trans-oceanic or trans-equatorial migrants.

The intervening "in-play" zones

Thus, on the long term if not necessarily on the very short term, each of the sardine–anchovy pair in each regional case can probably pretty consistently be the "superior competitor" in their respective natural "home segment" of their regional habitat. Otherwise, they should at some point have been completely eliminated from the regional system. An example of an anchovy "home segment" might be the western side of the Adriatic Sea, where Coriolis force causes the plume of the Po River, along with commingling waters from other rivers flowing out of the Dolomite Alps, to hug against essentially entire Italian coast of the Adriatic, while the upwelling-conditioned zone off the Croatian coast on the opposite eastern side of that sea may better represent natural "sardine waters". In the northwestern Mediterranean, the zones near the Rhone and Ebro River plumes would appear to be zones where the adaptations of the anchovy would tend nearly always to render it the superior competitor, whereas the vigorous turbulent eddy fields driven by the winter Tramontana/Mistral wind jets in the zone between may be difficult for anchovies while being manageable, and even offering favourable opportunities, to sardines. In the California system, the plume of the Columbia River and the run-off influenced near-coastal segments of the inner Los Angeles Bight (particularly before the impoundment of most natural run-off sources there) would seem to constitute favourable "home segments" for the respective northern and central subpopulations of northern anchovy (*Engraulus mordax*), while the offshore eddy fields and frontal systems where the upwelling-conditioned neritic waters meet the warmer, more saline oceanic water masses would seem to constitute sardine "home segments". [In view of considerations developed here, one may not find surprising the findings of van der Lingen *et al.* (2006) that natural selection has apparently optimized the digestive chemistry possessed by the two species groups to work particularly efficiently with respect to the size ranges of particles characterizing the "home segments" on which their viability may at times be totally dependent and to which the their respective physical capabilities appear likewise to have been optimized.]

The intervening zones of the rich regional upwelling or boundary current conditioned systems where the two species groups co-occur are intermittently dominated by one or the other of the groups, rather than being characterized by a single superior competitor. These intervening zones tend to be highly variable on a variety of scales. And so one might imagine that, as a result, the directions of the selection pressures may be highly non-uniform in both time and space. This may have suppressed, or at least delayed, development of specific adaptations to that intervening zone itself. In such a case, that rate of immigration of individuals from the nearby home-base segments could have been sufficient to overwhelm any nascent-specific adaptations to that zone within either of the sardine or anchovy generic groups.

To sum it up, we evidently have two species groups possessing differing strongly evolved adaptations simultaneously employing these adaptations to dominate, when possible, the richly productive but highly variable regional-scale habitats within which the more limited home-base segments of each are embedded (Figure 1). Whenever one or the other may achieve clear dominance, potential competitors for the dominant nektonic planktivore role are effectively eliminated, or at least "squeezed back" into primary home-base habitat segments that are particularly forgiving of their specific special problems and limitations. In the anchovy case, the home segment may be limited in extent while being subject to intense predation (e.g. from shore-based seabirds and marine mammals, near-coastal demersal "ambush" fish predators, etc.). In the sardine case, lack of consistent availability of adequate food concentrations in those outer reaches of the neritic system may limit their ability to grow abundance in the face of a spectrum of predator species that have been in diverse ways evolutionarily equipped to deal with the arduous local conditions. This is what appears to render the extensive breadth of rich but variable intervening habitat such a prize.

Excluding the "other"

The process by which the alternative member of the anchovy-sardine pair may be actually eliminated has been a puzzle. For example, why do the two species not simply separate spatially, each occupying a portion of the habitat where its adapted characteristics may render it comparatively superior on average? Rather, one of the species tends to become overwhelmingly dominant over the major portion of the shared habitat where the other "subordinate" species collapses to what might be considered a very low-abundance "refuge" level (Bakun, 2006a) where it may be found operating mostly within schools of similar-sized individuals of the much more numerous "dominant" species (Bakun and Cury, 1999).

Direct competition for food does not seem to be the answer. Nor does preferential predation on the other species' eggs and larvae (each appears to cannibalize its own potential offspring as readily as the others). The set of "school trap" and associated "school-mix feedback" effects (Bakun and Cury, 1999; Bakun, 2001, 2005a) could perhaps hold at least part of the answer. But one wonders if this group of mechanisms (even acting at several levels: adult energy efficiency, successful fertilization of eggs, larval mortality, etc.) by itself could be potent enough to produce the quite consistently repeatable, sweeping nature of the effect. The possibility of involvement of infectious diseases via cycles of increased population density, associated increased efficiency of disease transmission, resulting infectious outbreaks and subsequent population collapses has for some reason been largely neglected in discussions of this set of issues, but probably should not be discounted in terms of some degree of possible involvement in the alternating dominance issue (i.e. item "C" of the list presented in the Introductory section), but it is not easy to see how disease cycles could constitute any consistent rationalization for the other items (items "A", "C", "D", "E", etc.) for which we are seeking a comprehensive theory.

But, whatever the case, there can be no doubt that the very specificity of the respective anchovy and sardine adaptations must cause the two species groups to often react in strikingly differing ways to climatic or ecosystem variations. And we seem to drawn to a general conclusion that a major overall difference between the evolved ecological strategies of sardines and anchovies is that, of the two species groups, the sardine seems much more opportunistic with respect to major ecosystem variations. Anchovies, of course, are also *r*-selected (i.e. opportunistic) species, but in a different sense. That is, the sardine's evolutionary history has evidently provided characteristics by which radical ecosystem variation may represent distinct opportunities that the sardine may be prepared to actively exploit. In contrast, the anchovy's evolved characteristics may allow it to do rather well in a period of rather settled conditions or comparatively gentle, largely monotonic long-term trends in which it can take rather steady advantage of superior efficiency, but be unable to adapt to, and thus be seriously disrupted by, abrupt ecosystem change. Bakun and Broad (2003) illustrate this in terms of a financial stock market analogy, in which anchovies can be thought of as the "bulls" that do well in "good times" when conditions are benign, well behaved, and predictable, and sardines as the contrarian "bears" that during "bad times" are able to turn adversity into opportunity. To put this conceptual template in most simplistic terms, "normal" (i.e. stable or gently trending) favours the anchovy, whereas "disruption" (of the "normal") favours the sardine.

Resolving conundrums

So, if it is accepted that their differing evolutionary histories may have effectively assigned the ecological role of obstinate "robust strategist" to the anchovy and the role of "nimble opportunity-seeker" to the sardine, let us expressly test this "comparative advantage" template terms of its ability to yield a resolution of each otherwise puzzling pattern of interrelationship (i.e. the "conundrums" "A" through "E") outlined in the "Introduction" section. We briefly do this, item by item.

Item "A": sardines growing their abundance during poorly productive conditions

In the eastern Pacific, in both the California Current and Humboldt Current systems, anchovies do well in highly productive conditions that characterize the multiyear time intervals between *El Niño* episodes. This is as is expected for a species obviously oriented to highly productive ocean zones. A seeming paradox is that sardines, equally obviously adapted to highly productive ocean zones (upwelling areas, etc.), often do better, at least in the eastern Pacific, during the conditions of abruptly lowered local low-trophic-level productivity that characterize *El Niño* episodes (Niquen and Bouchon, 2004). The inference drawn by Bakun and Broad (2003), supported by the empirical finding of Agostini *et al.* (2007), is that *El Niño* disrupts the pervasive larval predator pressures that appear so damaging that many fish species (e.g. coral reef fish, tunas, salmon, etc.) make extraordinary expenditures of migrational energy and/or losses of reproductive product to remove their earliest life stages from proximity to high concentrations of potential larval predators. Sardines, particularly those of the genus *Sardinops*, apparently are able to employ their prodigious long-range swimming capabilities and widely ranging opportunistic migrational tendencies to ferret out isolated temporal-spatial "pockets" where a minimally adequate larval food concentration may be available. This may allow sufficient advantage to be gained from the reduced levels of predation such that their highly leveraged reproductive mode can generate a substantial degree of reproductive success even in the face of rather slow growth, etc., compared with that possible in much more productive non-*El Niño* conditions under which devastating larval predation might completely overwhelm any benefit from accelerated larval growth rate.

Item "B": the extreme fish productivity of the Peru–Humboldt LME

The evidently very benign situation off Peru may in large part be due to its low latitude position which results in strong upwelling-driven enrichment, uniquely long particle residence times, and low levels of turbulent mixing energy (Bakun and Weeks, 2008). These factors apparently combine to promote great abundances of diatom cells so large that they can be directly collected even by the particularly coarse filtering apparatus possessed by anchovies, while at the same time being harvested by a community of exceptionally large zooplankton that may constitute ideal objects of the raptorial feeding mode that appears the one most favoured by anchovies (van der Lingen *et al.*, 2006). Following each *El Niño* disruption during which the ecosystem had been cleansed of profusions of undesirable components, then reset and renewed, the system remains well behaved and predictable in a cyclical sense (i.e. in the more or less repeatable sequence of highly productive transients and the fact that when there is no active *El Niño* episode underway, differing intensities of the opposite *La Niña* state do little to seriously alter the basic benign situation). It represents the essence of "anchovy heaven" in which predators of anchovy larvae can be swamped by the shear productive energy of an explosively growing post-*El Ninõ* anchovy population. Therefore, the efficient anchovy can remain temporarily unimpeded in pursuit of its highly productive "robust" population strategy.

When the inevitable next *El Niño* does hit, the anchovy may be temporarily devastated. However, the sardine may turn the situation to its own distinct advantage by profiting reproductively from the associated reproductive failures of planktonic larval predator populations and of the absence of migratory nektonic predators that need much greater concentrations of zooplanktonic food than could be supplied from fish larvae alone and therefore may refrain from entering the habitat at all, either to feed or to deposit their voraciously predatory offspring. Moreover, the system cannot become durably stunted by development of malignant "eco-feedbacks", such as has been hypothesized for the northern Benguela (Bakun and Weeks, 2006), because of the periodic cleansing and resetting of the ecosystem by *El Niño*. [For expanded detail on the cyclic sequence of proposed interacting mechanisms underlying the overall highly productive Peruvian situation, one may refer to Bakun and Weeks (2008).]

Item "C": alternating dominance and item "D": basin-scale synchrony

This particular proposed pattern of interaction could also be expected hold on the longer multiannual to multidecadal time scales. For example, during the period from the early 1970s to the mid-1980s, the eastern Pacific upwelling systems appear to have become more dominated by influence of offshore-oceanic waters (Alheit and Bakun, 2009), similarly characterized by smaller food-particle spectra, etc. (To what extent this might represent some separate truly longer term phenomena at its base, or be largely a simple effect of a period of raised frequency and strength of individual *El Niño* episodes is unclear.) But whatever the precise nature of the cause, it can be understood why anchovies, when food particles become too small to be effectively filtered by the gillraker structures of anchovies, might give way to the finer filter-mesh-bearing sardines. In general, this set of considerations would appear to offer an answer to the alternating dominance issue for the eastern Pacific systems, at least for the period following 1970 that is the period for which the indication of alternating dominance may be truly credible (Bakun, 2005b).

But how does one explain the northwestern Pacific? As stated earlier, in the neritic ecosystem of the northwest Pacific near Japan which is under the influence of the extremely energetic Kuroshio western boundary current system, the anchovy never approaches peak-abundance parity with the sardine (as is also the case in the particularly energetic upwelling system of the northern Benguela region). In these systems, the anchovy has seldom assumed a position of true dominance other than by virtue of the sardines' abundance falling very low. According to our inferred conceptual template, sardines appear evolutionarily particularly well-equipped to take opportunistic advantage of system disruptions. The strong flows and intense turbulent eddy characteristics of these particularly energetic systems appear to offer continuous patterns of disrupted conditions in time and space of exactly the sort that the sardines' evident adaptations seem designed to accommodate.

More than 30 years ago, Skud (1982) had already identified a general pattern in a variety of fish that seem to form interrelated "pairs" (as anchovies and sardine seem to do), such that the population dynamics of the dominant species tends to respond to environmental factors, whereas those of the subordinate species respond to the abundance variations of the dominant one. Therefore, if we assign the dominant wasp-waist role in the neritic ecosystem near Japan as characteristically belonging to the sardine due to the intense nature of the Kuroshio system in which the regional-scale population at least partially operates, the observed out-of-phase alterations fall directly within Skud's identified pattern.

The early 1970s to mid-1980s period, during which sardine populations exploded all around the rim of the Pacific, was characterized by a steep decadal scale decline in the Southern Oscillation Index (SOI) that would of course have been related to an unusual combination of frequent and intense annual-scale declines (i.e. of *El Niño* episodes). Thus, the enhanced "El Niño" character of this period would naturally seem (see discussion of "item A" above) to favour sardine population growth in the eastern Pacific, if only in terms of a sum total of an increased frequency of successful annual growth episodes. Moreover, the long trend that culminated in a distinct change in the "mean level" of the various indices undoubtedly represented a degree of continually developing reorganization of various ecosystem distributions and relationships that probably involved significant natural evolutionary selection of many short life cycle ecosystem components. The sardine's intrinsic exploratory, opportunistic tendencies, and capabilities would be expected to be invaluable in tracking a favourable ecological response to the rapidly reorganizing ecosystem context (as expressed in our simplified "comparative advantage" conceptual template, i.e. that "disruption favours the sardine").

Moreover, in addition to the uniquely steep decadal scale long-term trends of the early 1970s to the mid-1980s interval ("boxed" in Figure 2b), the period appears also to have been subject to uniquely energetic shorter 1- or 2-year interannual-scale climatic gyrations. For example, if one counts all the 1- or 2-year incremental differences in the various smoothed 51-year (1950–2001) series of annual climatic indices assembled in Figure 2 of Tian *et al.* (2004) [more recently also reprinted as Figure 2 of Alheit and Bakun (2009)], the 13-year (1970–83) segment contains: (a) the largest ('81–'82), the 3rd largest ('75–'77), the 4th largest ('72–'74), and the 5th largest ('70–'72) in the entire 51-year annual mean SOI series, (b) the largest ('77–'79), the 2nd largest ('70–'72), and the 4th largest ('82–'83) in the winter North Pacific Index series, (c) the largest ('76–'77) and the 2nd largest ('70–'72) in the winter Pacific Decadal Oscillation series, (d) the largest ('76–'77) in the winter Arctic Oscillation series, and (e) the largest ('77–'79) and the 2nd largest ('73–'74) in the winter Monsoon Index series. Again the pattern that "disruption favours the sardine" emerges very distinctly.

In summary, the continual climatic disruptions that appear to have the characterized the early 1970s to mid-1980s period, coupled with the inference that "disruption favours the sardine", appear to offer a linkage mechanism for the synchronous dynamics of the widely separated sardine populations located in the far corners of the Pacific basin. This coupled with the observed pattern of

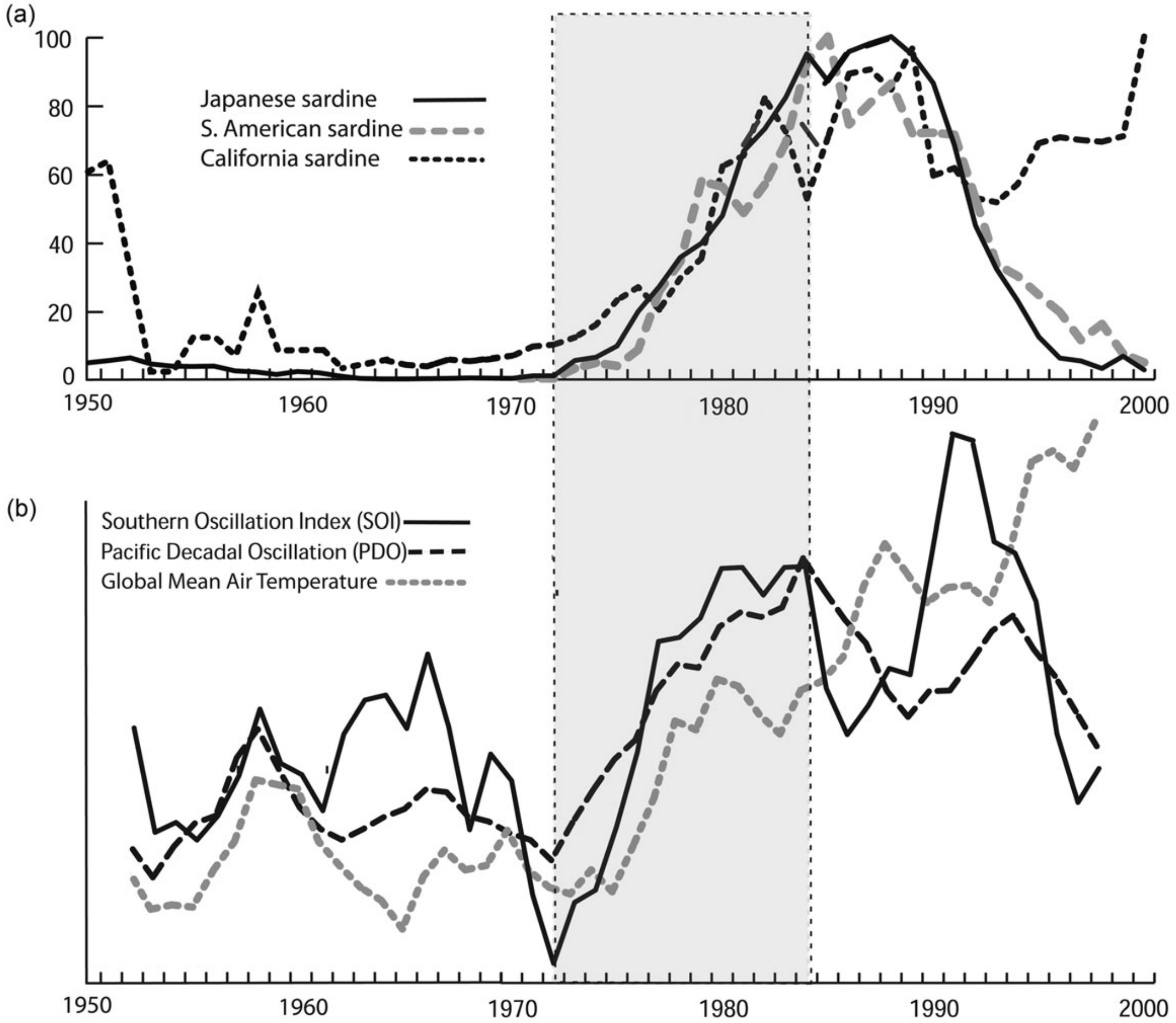

Figure 2. (a) Variations in the abundance of the largest sardine stocks of the Pacific Ocean plotted as percentages of maximum annual values for the period 1970–2000, based on landings data taken from the FAO files. (Before the 1990s, most California sardine landings were taken by the Mexican fishery inside the Gulf of California; beginning in the mid-1990s increasing contributions came from US and Canadian fisheries.) (**b**) "Low-passed: (via 5-point running means of annual mean values) versions of several prominent climatic index time-series. The shaded rectangle indicates the early 1970s to mid-1980s period of steep decadal-scale trends discussed in the text. (Panels redrawn and extended from Bakun and Broad, 2003).

out-of-phase population variations of anchovies and sardines (Item C, in our list above) would then work together to rationalize the observed basin-scale synchrony (Item D).

Item "E": the "Law of two"

So finally we come to the intriguing item "E" in the list given in the "Introduction" section. Why are there usually two dominant small pelagic species, an anchovy and a sardine, rather than just a single species that turns out to be the superior competitor in each local situation? And why would this intriguing "law of two" seem to hold, not only in highly productive temperate coastal upwelling ecosystems and in the likewise highly productive but dynamically quite different western boundary current situation of the northwest Pacific, but also reportedly in rather oligotrophic semi-enclosed peripheral seas such as the Mediterranean. Even within sub-basins of the Mediterranean, this "law of two" seems to hold in such quite differing physical/ecological situations as the Balearic and Adriatic Seas. Moreover, if more than one species, why not more than two? For example, a "cyclic advantage"-type explanation would require at least three competing species (Matsuda *et al.*, 1991; Sinervo and Lively, 1996).

A possibility is that there are ordinarily two, and only two, sufficiently distinct "home-base" habitat segments in any of these boundary ecosystems. One of these is characterized by terrestrial influences, significant turbidity, large suspended organic particles, etc. Here, the anchovy is superior and efficiently outcompetes any interloping other species of small pelagic planktivore. The other sufficiently distinct segment is at the nebulous, uncertain, temporally, and spatially extremely patchy offshore edge of the ecosystem where neritic and oceanic effects merge together. Here, opportunism and flexibility is at a premium, and food particles may typically be very small. Here, the sardine has the ability to "hang on" where potential small pelagic competitors (vertically migrating mesopelagic fish representing an essentially different strategy that does not truly compete with that of the sardine) and extremely damaging concentrations of predator stocks cannot.

Therefore these two alternative species groups, anchovy and sardine, could be available and ready at any time, when conditions enable, to break out of their respective "home-base" habitat segments and seize dominance of the extensive intervening in-play zone ("Item 'C': alternating dominance and Item 'D': basin-scale synchrony" section) of the neritic habitat. According to the conceptual framework being inferred here, the enabling conditions for anchovy breakout might be a period of adequately vigorous primary productivity during which system disruptions tend to be minor (e.g. when after an *El Niño* episode, the system has stabilized and vigorous primary production resumes). Sardine breakout evidently may be favoured by a major system disruption such as an abrupt drop in primary production (as during an *El Niño* episode in the eastern Pacific) or by a period of steep trend of change (i.e. continuously progressing disruption) in which a capacity for nimble opportunism may be at a particular premium.

A separate sardine genus for the North Atlantic

The inference that sardines may depend on system disruption to most effectively exert their evolved opportunistic advantages might derive further credibility from the total absence from the North Atlantic basin of sardines of the genus *Sardinops* that have very successfully colonized the suitable temperate neritic boundary habitats in the Pacific (both hemispheres) and south Atlantic basins (*Sardinops* having been the basis of most of the inferences we have drawn with respect to sardines). Most knowledgeable colleagues could probably agree that *Sardinops* may exhibit opportunistic characteristics to a somewhat greater degree than does *Sardina* (certainly, *Sardinops* seems to be much more migratory of the two, as well as much more prone to abrupt distributional expansions and contractions). *Sardina* is the temperate sardine genus that is currently established in the North Atlantic basin which, of all the major ocean basins on earth, is the one most influenced by continental effects. Land surface possesses little heat storage capacity to serve as "climatic memory", whereas water in its liquid state has a notably large heat storage capacity. The much larger areas of heat-storing ocean surface compared with land surface in the Pacific and in the southern hemisphere ocean basins allows the climates of these zones to "wander" on multiannual scales much more than in the North Atlantic area, where the interaction of heating and cooling of stationary continental landmasses with a quite precisely cyclic seasonal progression of height of the sun may force the local ocean climate into greater interannual regularity compared with the very large seasonal amplitudes to which the local ocean ecology must be adapted. Thus, one might speculatively conclude that the evolved opportunistic capabilities of the genus *Sardinops* could be less decisive in the North Atlantic than in the other major basins. Indeed, perhaps much of the evolution of the genus *Sardina* might actually have been based within the unique conditions of the Mediterranean where the external climate is dominated by continentality while the liquid-water environment exhibits a particularly "oceanic" character due to the relative nutrient impoverishment produced by the "negative estuary" mode of water exchange with the North Atlantic proper. In the continentally influenced North Atlantic, which may thus be less subject to interannual variation in the degree of its system disruption, the genus *Sardina* might simply manage to outcompete the genus *Sardinops* in the characteristic "sardine home-base" habitat segments on the European side of the North Atlantic. The western side of the Atlantic, with its shallow broad continental shelf and very high volume of continental run-off, may simply lack significant "home-base" habitat for sardines.

Implications for effects of projected climate changes

The foregoing process of step-by-step rationalization of the list of prominent conundrums (Subsections "A" through "E", above) corroborates the earlier gross characterization (that was based on comparative morphological and behavioural aspects, as well as on inferred evolutionary, aspects) of anchovies as "efficient stay-at-home specialists" and of sardines as "nimble wide-ranging opportunists". Based on this characterization alone, one could guess that sardines might fare better than anchovies as rapid global changes transpire. However, our analysis has also pointed out a "home-base" anchovy environment as being one conditioned by continental run-off. A fairly recent consensus among climate models (Meehl *et al.*, 2007) indicates that on a global-average basis, as greenhouse gases continue to accumulate in the earth's atmosphere, precipitation will generally increase. This would tend to offer new or enhanced estuarine and coastal run-off-affected zones where anchovies may turn out to be superior competitors. However, the model consensus also suggests that a greater proportion of the subtropics may be affected by drought, which according to the framework developed herein should favour sardines. This tendency for moist regions to become wetter while dry regions become drier is in fact captured by the observational record as well as by models (John *et al.*, 2009). Moreover, due to the increased atmospheric water vapour available to be released from a warmed atmosphere as precipitation due to orographic effects, the increase in rainfall amount is likely to be larger on the windward slopes of mountain ranges (Christensen *et al.*, 2007). Mountain ranges border some of the most important marine ecosystems having wasp waists dominated by the sardine–anchovy species pair. In particular, increased rainfall in the near-coastal zones of Ecuador and Peru, as well as all along the Asian continental boundary of the northwestern Pacific, is indicated in the IPCC Regional Climate Projections (Christensen *et al.*, 2007). Increased precipitation is also projected by IPCC along the North American Pacific continental boundary north of 40° latitude except during summer and, in the northwestern Atlantic, throughout the year along the coasts of the North and Baltic Seas; thus, in these areas, as the anchovy–sardine complexes expand northwards due to warming, they will be expanding into areas where precipitation is expected to be increasing as climate change proceeds, potentially favouring anchovies.

This example discussion has of course only scratched the surface in terms of available material for such speculative inferences. To briefly mention another aspect, one currently prominent climate change projection is that the Pacific trade wind circulation may decline as climate change proceeds (Vecchi *et al.*, 2006). The implication would seem to be that the ocean–atmosphere system of the Pacific might shift in the direction of a more chronic, if "low-level", *El Niño*-like state. If so, since *El Niño* conditions have seemed to favour sardines over anchovies on both sides of the Pacific, this aspect might be expected to benefit sardines. But it might presage less intense individual *El Niño* episodes, which could lessen the "boom or bust" aspect of eastern Pacific marine ecosystems, i.e. perhaps leading to lowered base populations of seabirds and marine mammals, but conceivably to fewer or less serious incidents of periodic starvation of these highly visible "charismatic" species. Yet, another projection that has been put forth is that upwelling may intensify in the "classical" upwelling ecosystems as climate change proceeds (Bakun, 1990; Diffenbaugh *et al.*, 2004), although it should be said that that particular prognosis remains somewhat controversial (Bakun *et al.*, 2010; Wang *et al.*, 2010). If so, among other major trophic consequences, because of the greater difficulty zooplankton have in maintaining population against increased offshore transport associated with intensified upwelling, the ratio of phytoplankton to zooplankton might be expected to increase (Bakun *et al.*, 2010). This result, as well as the fact that anchovies seem to be somewhat less well adapted to intensified flow systems, would again seem to generally favour the more omnivorous highly mobile sardines over the largely zooplanktivorous, weaker-swimming anchovies. The implications are obvious, important, and diverse, e.g. on aspects including hypoxia, marine "dead zones", red tides, etc., in addition to distinct effects on spatial aspects of ecosystem support to fishery resource dynamics, etc. (the very heavy use of "etc." reflecting the very broad choice of potential examples relative to the space that can be afforded to them in a treatment such as this).

The salient point here is that a simple conceptual framework such as has emerged from this limited discussion may provide one type of reference with which to try to gauge and begin to understand the nature and significance of developing patterns in ecosystems featuring the anchovy–sardine species pair.

Will active opportunist species "steal the stage"?

The early 1970s to mid-1980s period (highlighted in Figure 2), in which simultaneous sardine population explosions coincided with steep decadal scale changes in levels of various climatic indices, has featured prominently in our characterization of sardine as being adapted to a rapidly changing (i.e. "disrupted") situation. Interestingly, this same period also featured strikingly similar "breakout" population increases and following declines in quite a large number of other marine species, particularly within the Pacific Ocean basin [for references, see Benson and Trites (2002) and many sources cited therein] but also more generally scattered throughout the entire global ocean system [for references and sources for additional citations, see Bakun (2005b)]. These included some of the largest, most important fishery resource populations in the North Pacific zone (e.g. Alaska pollock, sockeye salmon, pink salmon, chum salmon, yellowfin sole, Pacific hake, Pacific cod, and many others). In the tropical Pacific Ocean, additional examples included yellowfin and skipjack tunas, various lobsters, seabirds, and coral reef fish, and even phytoplankton and zooplankton distributions. Apparent echoes of this pattern in the Atlantic have involved various stocks of northern cod, as well as extraordinary outbreaks of normally rather uncommon fish species such as triggerfish and snipefish. This leads to an intriguing question. Might the stocks of other species that mirrored the sardine rises during that unique period of steep climatic trends potentially be likewise viewed as "active opportunist" species? And might stocks that appear to have acted during that period in an opposite "anchovy" sense perhaps be usefully viewed, at least hypothetically, as "efficient specialists" that may react adversely to rapid ecosystem changes, but might be able to outpace their less efficient rivals in tracking somewhat more gradual ecosystem trends? If so, we perhaps will have found a sort of new "philosopher's stone" for turning ostensibly random information into distinguishable emerging patterns that may aid recognition of some overall order within the apparent chaos of complex-adaptive marine ecosystem responses.

An initial step could be examination in a similar manner to that illustrated here (e.g. gleaning some enhanced mechanistic understanding via rationalization of existing apparent conundrums in each case, etc.) of each of the species groups and ecosystem types conforming to the same sequential pattern. Undoubtedly such an interregional pattern–recognition exercise could constitute fascinating collaborative intellectual activity. And if successful, and appropriately coordinated, the effort might well contribute towards significantly accelerated understanding and enhanced prediction skill during the coming challenging period of rapid global changes. [One may guess that a similar envisioned need for a coordinated "broader view" of marine ecosystem operation may have been what led Johan Hjort to become a "founding father" of the International Council for the Exploration of the Sea (ICES), within which he served as the Norwegian delegate from its founding in 1902 to 1938, when he was elected ICES President, a position he held until his death in 1948.]

Given the vexing lack, in the full century that has elapsed since Hjort's landmark publication, of substantial progress by the "applied science of fisheries oceanography" towards its major goal of improving fisheries management and marine conservation (Hare, this volume; Houde, 2008), a greater degree of "outside-the-box thinking" would seem to be called for. Hjort's celebrated contemporary, Albert Einstien, is said to have remarked that "The eternal mystery of the world is its comprehensibility". So why has not fishery oceanography produced the sort of revolutionary advances in applications that other sciences have? In answer, it might perhaps be appropriate to cite a second quote from Doctor Einstien: "things should be made as simple as possible, but not simpler".

The currently prevalent reductionist approach addresses an expanding multitude of potential simple mechanisms, each of which is likely to be more or less active at one time or other. One can of course model and simulate these *ad infinitum*. But since the important events to be understood and ultimately predicted (population collapses, etc.) seem most often to occur on interdecadal time scales, one wonders how the multitude of interacting factors could ever be sorted out sufficiently confidently to support strong corrective actions (Bakun and Weeks, 2006), even in the unlikely event that the system structures would be stationary in a temporal sense, which would seem unlikely in this era of progressing global environmental change? It seems in fact that fisheries oceanography may be caught in a sort of quagmire in which ever more resources seem to be required to follow an ever more reticulated path that seems never to get us much closer to its major goal. Thus, it may be useful to seek more integrated, more holistic approaches wherein an expanded "universe" of diverse experiences might be assembled together within innovative conceptual frameworks that could facilitate recognition of informative emergent patterns ensuing from the superposition of multiple hierarchies of interacting component mechanisms. The notion elaborated in this paper of classifying fish populations according to apparent degrees of evolved opportunistic capabilities and behaviours might perhaps be considered as one possible initial step, even if only a "baby step", in that direction.

Concluding remarks

Some readers might feel frustrated that this attempt at a synthesis focusing on anchovies and sardines may not have pointed very directly to any concrete model supporting specific predictions with respect to that particular pair of species groups. But as stressed in the introductory section of this discussion, we seem to be dealing with complex adaptive systems that may be governed ultimately by nonlinear feedbacks. Therefore, earlier hopes for effectively employing a linked sequence of simple linear models appear to be receding (MacCall, 2009b). Drawing a musical analogy, one might say that to a careful "listener", the real generative action in the ocean system may play less like a set recipe and more like a complex symphony, replete with shifting rhythms and haunting, often scarcely perceived, recurring themes that may never be precisely repeatable.

Does such a realization signify defeat? One would think not. It just might have to be accepted that a better approach may be one much less focused on specific model-based predictions and annually reformulated management advice, but rather more directed towards an acquired level of understanding and accumulated experience that supports reasoned expectations as to the "probability vs. consequence" spectrum of potential outcomes of actions undertaken. One simple illustrative example taken from an entirely different context may be that of a particular antibiotic (a different type of likewise valuable, but destructible, resource). One may not be able to reliably predict precisely when a certain antibiotic will begin to fail. But sufficient understanding and experience have accumulated to point out what will make it fail more rapidly (e.g. feeding it to pets and farm animals, ceasing use before a prescribed course of treatment has been completed, etc.). As Houde (2008) has expressed it "Understanding the causes of recruitment variability is a desirable goal; 'solving the problem' may be an unrealistic goal".

The value of seeking a spectrum of outcomes, as opposed to narrowly focusing towards identification and elaboration of a most probable outcome, is worth stressing. For example, can one afford to focus totally on maximizing of production of a particularly favoured resource species while ignoring significantly less likely but perhaps much more menacing possibilities (such as transformation of the wasp waste of an ecosystem to durable dominance by infestations of jellyfish, or by hypoxia-producing bacteria, etc.), which may be potentially lurking as yet unrealized out in the tails of the probability distributions?

Thus, in the future, instead of management advice that sounds like "Do such and such, just do not deviate from the plan, and all will be well", truly well founded advice may sound more like "Well, no one can be sure precisely what will happen, but the last several times someone tried what you propose, differing things happened, but in general, no one was particularly happy with the way things worked out". If we are to succeed in preserving our beautifully intricate ocean systems, we must hope to at least advance to that basic level. And, happily, advancing to that level should lie within our scientific reach. From a personal and professional standpoint, "getting there" should continue to be an extremely engrossing and fascinating activity.

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Handling editor: Howard Browman

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2293–2299. doi:10.1093/icesjms/fsu158

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Where we are going

Food for Thought

Where has all the recruitment research gone, long time passing?

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Rice, J., and Browman, H. I. Where has all the recruitment research gone, long time passing?. – ICES Journal of Marine Science, 71: 2293–2299.

Received 15 August 2014; accepted 18 August 2014; advance access publication 8 September 2014.

For most of the past 100 years, research into recruitment processes—as pioneered by Johan Hjort—has been a consistent focus of research in fisheries science. This was reflected not only in the literature but in the organizational structures and research strategies of national and international fisheries research and management institutions. Over the past decade or so, we perceived that recruitment research is fading, if not into obscurity then at least into a more marginal place in fisheries and marine research. In this paper, we assess if our perception is real by quantifying trends in scientific publications and in the work activities within ICES during specific periods extending back to the 1920s. Our analysis documents a decline in research on recruitment processes. We put forward three possible hypotheses to explain this decline: 1. *All the key research questions about recruitment have been answered*; 2. *The volume of research on recruitment processes has declined because the answers are no longer relevant*; 3. *Recruitment research has been co-opted by more trendy, possibly ephemeral, and research topics*. There is little evidence to support the first two of these hypotheses and we consider the third to be the most plausible. Finally, we conclude that this new terminology/repackaging of recruitment research does not bring with it new and fresh thinking and, therefore, comes at a cost that should be carefully considered.

Keywords: climate change, ecosystem-based management, fish population dynamics, integrated assessments, Johan Hjort, recruitment variability, research prioritization in marine science.

Introduction

Johan Hjort studied the processes driving recruitment and population dynamics of fish, and his benchmark publication (Hjort, 1914) has provided a foundation and impetus for 100 years of research. The penetration and influence of Hjort's (1914) treatise has been remarkable (Aksnes and Browman, 2014). One century after its publication, it continues to be cited frequently, with citations having appeared in over 150 journals covering fisheries (22 journals), marine science (71), general ecology (23), general science (35), statistics and modelling (5), and even fields as distant as biomedicine.

For most of the past 100 years, recruitment processes has been a consistent focus of research in fisheries science. This was reflected not only in the literature but in the organizational structures and research strategies of national and international fisheries research and management institutions. Over the past decade or so, we perceived that recruitment research is fading, if not into obscurity then at least into a more marginal place in fisheries and marine research. "Recruitment" has become a modifier, or dependent clause, describing research that has some other focus, commonly something current such as climate change, the "ecosystem approach" or "integrated assessments". We interpret this observation to reflect a basic change in what is driving marine research—in the past, the driver was mainly bottom-up: the curiosity, ideas, and hypotheses of scientists determined what research was conducted. In the present, the driver is mainly top-down: large international government organizations and non-governmental advocacy groups drive research questions by allocating research funding in a short-term socio-economic and political framework and this determines what research is conducted. We will take up this change in what is driving the foci of our research activities elsewhere.

Adoption of the ecosystem-based approach to fisheries management (EBFM) was intended—at least conceptually—to significantly broaden the information, biophysical processes, and ecological concepts taken into account in the management of living resources. Hence, EBFM is at least a possible cause of a shift in the focus of fisheries research. According to FAO (1995, 2003), one of the basic pillars of EBFM is to take environmental drivers of stock dynamics into account. However, this emphasis on environmental drivers might have either increased the importance of recruitment research as a key pathway through which the drivers are experienced, or decreased its importance through empowering many other ecosystem factors to share the research spotlight with recruitment research. It is noteworthy that EBFM was adopted by national and international marine resource management institutions by mandate from the very top levels of international policy making (Browman and Stergiou, 2004, 2005). EBFM was adopted before most "bench-level" researchers actually knew what it was. What it actually is has yet to be completely worked out (it would not surprise us if we move on to something else before that actually happens—see Link and Browman, 2014). We view this is a seminal example of top-down-driven marine science. Climate change and high-profile offshoots such as ocean acidification are also deflecting the focus away from recruitment research, although again recruitment processes may be one of the common ways that climate effects are manifested in population and ecosystem dynamics.

In this essay, we first ask if the repackaging of recruitment research that we describe above is real. We assess this by quantifying trends in scientific publications and in the work activities within ICES during specific periods extending back to the 1920s. We then asked what the drivers of this trend are, and what the influence of those drivers on fisheries research might be. We also discuss whether this trend should be considered a good thing in that it represents a divesting of a century-old framework of hypotheses for understanding recruitment variability that has proved increasingly cumbersome and unhelpful or, alternately, that it is not such a good thing because it has resulted in a loss of focus on questions that are at the very heart of fisheries research (see Hare, 2014).

Methods

Orientation. Our objective is to get readers to think about what, if anything, has happened in recent years to the traditional focus of fisheries research on recruitment processes. Our analysis could not be exhaustive. However, by focusing selectively on key fisheries terms and phrases from several relevant sources, we were able to assess whether or not any trend exists. We selected the year 2000 as the beginning of the postulated shift in focus away from recruitment research. That choice is based upon the dates of the Reykjavik Declaration (2001) and the 2002 World Summit of Sustainable Development, important policy benchmarks that installed EBFM as the international framework for the management of living marine resources (Rice, 2014). All decisions about the analytical approach (e.g. periods selected, search terms, etc) were made *pre factum* and were not modified *post factum*.

Indicator 1: historical trends in citations of Hjort (1914) and in recruitment research

We used two approaches to assess whether there have been historical changes in the intensity of recruitment-related research. First, the number of citations to Hjort (1914) were obtained from Thomson Reuters's Web of Science (WoS) using the database citing reference function. These were tabulated by year, but only back to 1950 because of uncertainties about the extent of journal coverage before then. To normalize for the overall increase in the number of publications in marine science, the WoS was used to obtain the number of publications per year that were retrieved using "marine" or "fisheries" as keywords in the topic search field. Although the search extended back to 1950, only results from 1970 onwards were used because of incomplete journal coverage in the WoS before that year. For the period 1970–2012, an overall linear regression was fit to publications-per-year citing Hjort (1914), and to the annual ratio of publications citing Hjort (1914) to the total number of publications retrieved by the keywords "marine" or "fisheries" (we consider the latter indicative of the trend in publications that might consider Hjort (1914) relevant). A second pair of regressions were fit to the periods 1970–1999 and 2000–2012 to see if there has been a recent change in those trends. The degree to which the piecewise regression improved fit to the data gives some indication of how different the recent trends are from earlier ones (taking the larger number of parameters to be fit with piecewise regression into account using Akaike information criterion; Burnham and Anderson, 2002).

Second, archived issues of the *Transactions of American Fisheries Society*, the *ICES Journal of Marine Science*, and the *Canadian Journal of Fisheries and Aquatic Science* were accessed and all articles from three decades of interest were examined: 1925–1934, 1979–1988, and 2002–2011. The decades of interest were chosen as being relatively soon after the publication of Hjort (1914), but long enough after for there to have been penetration of the ideas presented into fisheries research, the decade immediately following extension of jurisdiction with UNCLOS when there was great interest in fisheries and marine research generally, and finally the decade after the adoption of EBFM. Only the materials classified as research articles by these journals were included in the analysis. For articles accompanied by abstracts, the abstracts were sorted based on a keyword search (recruit*) then scored depending on whether the study was primarily concerned with recruitment variability (high score), addressed the topic of recruitment in some capacity (low score), or did not relate to recruitment (no score.) For articles without an abstract, the same analysis was completed by scanning the body of the article. Titles of articles in the two more recent decades that were not returned in the keyword search were scanned and scored for relevance as described above. All articles in the earliest decade were scanned in this manner, if the term "recruitment" and its derivatives had not penetrated the literature. Once all articles were scored, results were expressed as a percentage of total research articles published per journal, per decade, with high-scoring articles given full weight (1.0) and low-scoring articles given less weight (0.5). A total of 10 898 articles were examined.

Indicator 2: prominence of recruitment research in ICES activities throughout its history

Three periods were selected for assessment: 1925–1934, when we considered that research collaboration in ICES (and investments by members) had fully recovered from the effects of the first world war but were not yet being affected by the lead-in to the second world war; 1985–1989, when we considered research programmes would have adjusted to the added responsibilities of extended national exclusive economic zones but not yet been dominated by the coming crises in groundfish stocks; and 2008–2012, the most recent period. The first period was longer than the other two in order that the total number of activities considered during each period was comparable. Sources of information for this analysis were the nature of the work reported to ICES in either the annual Procès-Verbaux (1925–1934) or Expert Group CR documents

(1985–1989), or the tasks assigned to ICES Expert Groups in their Terms of Reference (2008–2012). Methods of information extraction and statistical comparisons are described in detail in the Supplemental Material.

Indicator 3: the importance and precision of recent recruitment estimates

We extracted the proportion of the fishable numbers composed of new recruits, and the uncertainty of those estimates, for the final assessment year (usually 2012) of the most recent benchmark-scale assessments of 24 stocks, six each from the ICES Northeast Arctic and North Sea regions and from the US New England/Gulf of Maine and Bering Sea/Gulf of Alaska areas (listed in Supplemental Material). Each was a major stock for the region. A scatterplot of the percentage of numbers-at-age in the fishable stock that are new recruits against the coefficient of variation (CV) of the estimate was generated to illustrate the degree to which recruiting cohorts contribute to fisheries and how accurately assessments estimate the sizes of these recruiting cohorts for these 24 "flagship" stocks. No statistical analyses of the ratios and CVs were undertaken because of the *ad hoc* manner in which several of the stock-specific CVs were estimated. Moreover, because of interannual variation in recruiting year classes, had a different year been chosen from the numbers-at-age vector, the ratios on the *x*-axis would have been different as well. Therefore, this material is not presented as a quantitative result but is rather used illustratively in Discussion.

Results

Historical trends in citation of Hjort (1914) and in recruitment research

The absolute number of citations to Hjort (1914) increased significantly from 1978 to 2012 (Table 1 and Figure 1). However, scaling citations to Hjort (1914) against the total number of publications in marine science in each year reveals different trends with time: between 1978 and 1990, the proportion of publications that cited Hjort (1914) increased significantly, while from 1991 to 2012 it decreased (Table 1 and Figure 2). This proportional annual decline by ~2 expected citations per year at recent total publication rates has been stable for the past 20 years. We note that there was a doubling of "marine" publications from 1990 to 1991—although this is difficult to explain, it seems likely that it is due to a change in journal coverage by the WoS.

The percentage of articles that were related to the topic of recruitment variability published in *Transactions of American Fisheries Society* and the *ICES Journal of Marine Science* as a proportion of all the articles published in those journals decreased from the earliest through the most recent decade of interest, although it has remained stable in the *Canadian Journal of Fisheries and Aquatic Science* (Figure 3).

Table 1. Statistical results of regressions of absolute numbers or proportions of publications in scientific journals that cite Hjort (1914), over various time intervals.

Attribute	No. of citations[a]	Proportion citing Hjort[b]	
Time interval	1978–2012	1978–1990	1991–2012
Slope	1.155	0.00133	−0.000146
Intercept	3.897	0.00133	0.00626
d.f.	34	11	21
Probability	<0.001	$0.01 < p < 0.05$	<0.01
% variance explained	0.829	0.271	0.614

[a] Number citations per year citing Hjort (1914).

[b] Proportion of all marine or fisheries papers citing Hjort (1914).

The role that recruitment research has played in ICES work

The results of the inventories of total activities reported in ICES outlets appropriate to the three selected periods, and the number of those activities that might be considered to contribute to research on recruitment, are presented in Tables S1–S3 of the Supplemental Material. Because of the different sources of records of activities during the three periods, no overall comparisons were undertaken. However, individual proportions can be compared both within and across the three periods.

Overall, a significantly lower proportion of ICES work was related to recruitment research in the late 1980s (Supplementary Table S2) than in the 1920s and 1930s (Supplementary Table S1), and the proportion of all work (ToRs) considered possibly related to recruitment research was significantly lower in 2008–2012

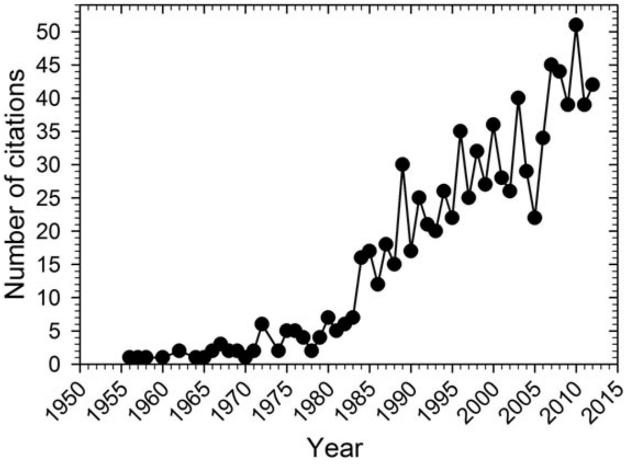

Figure 1. Absolute number of citations to Hjort (1914) per year (1956–2012) from the Thomson Reuters Web of Science database.

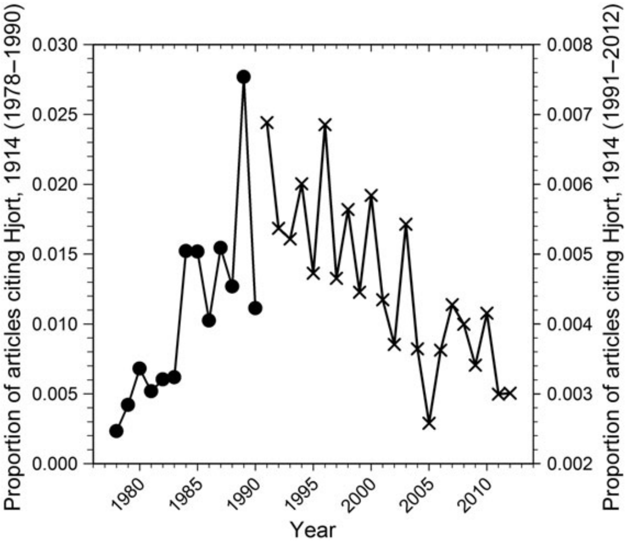

Figure 2. Citations to Hjort (1914) as a proportion of all publications in marine and fisheries science from the Thomson Reuters Web of Science database. Data are for 1978-1990 (solid circles,scale on left) and 1991–2012 (crosses and scale on right).

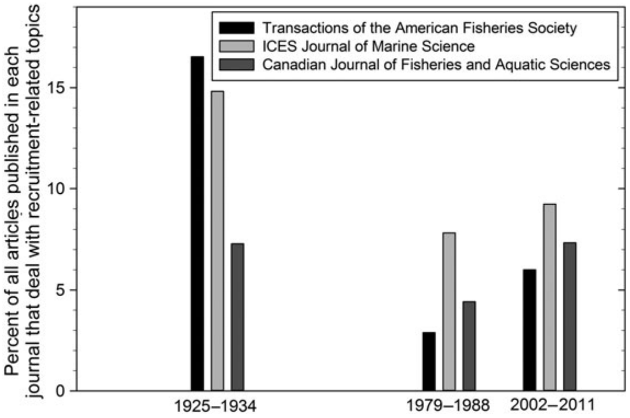

Figure 3. The percentage of all articles published in three fisheries science journals during three decades (1925 – 1934, 1979 – 1988, and 2002 – 2011) that deal with "recruitment"-related research topics.

(Supplementary Table S3) than in the late 1980s (Supplementary Table S2). The comparisons presented in the Supplemental Material show that some of the decline in the importance of activities relevant to recruitment research in ICES has been due to an increase in the dominance of activities directly feeding assessments and other advisory demands. Since the 1990s, however, even among non-advisory work, the importance of recruitment-related activities has dropped significantly, after representing nearly a quarter of ICES work for over 60 years.

The importance and precision of recent recruitment estimates

A review of the age composition of the 2012 populations of 24 flagship fish stocks from two major stock assessment authorities (ICES and the United States National Marine Fisheries Service) shows that new recruits comprised at least 20% of the fishable population in two-thirds of the stocks (Figure 4). Five stocks had <10% of the fishable population comprising new recruits (Figure 4). However, this reflected interannual variation in year-class strength, not fisheries targeting the older fish in the population. In the three stocks with the lowest percentages of new recruits in the fishable biomass in 2012 (North Sea Herring, Georges Bank Herring, and Northeast Arctic Coastal cod), it is noteworthy that, had the calculations been made for the 2011 population, new recruits would have constituted ~53, 35, and 11%, respectively, of fishable numbers (see Supplemental Materials). Not only is year-to-year variation in recruitment large but annual estimates of recruitment are associated with CVs of 30% or more; larger than the CVs of older ages in the assessment (Figure 4).

Discussion

Our first two indicators, based on historical patterns in publications and ICES work related to recruitment processes, indicate that research on recruitment, while not fading into obscurity, is declining in relative importance and in visibility. Indicator 1, the likelihood that the seminal article by Hjort (1914) will be cited, has declined significantly since 1990, after increasing in the decades before that. In addition, the relative proportion of articles about recruitment appearing in two of the main fisheries journals has declined. Indicator 2, ICES work possibly relevant to recruitment research comprised approximately one-quarter of all ICES non-assessment work from the 1920s to the end of the 1980s, but by the most recent 5-year period had declined to barely 10%. This decline is amplified when all the ICES work related to advisory activities is considered, reducing recruitment-related ToRs to barely 5% of all work, even when applying a very generous standard for relevance to recruitment. Although we have not quantified it here, a quick look at the organizational structures and scientific work plans of the world's major marine science/fisheries institutes reveals that the term "recruitment", and terms associated with it, have essentially disappeared. This is exemplified by Johan Hjort's own home institute in Norway—the Institute of Marine Research—and by the research centre that bears his name, the "Hjort Centre for Marine Ecosystem Dynamics". Interestingly, when the Hjort Centre was first proposed in 2005 its name was "Johan Hjort Centre for Fish Recruitment Research" (HIB was a member of the writing team for that application).

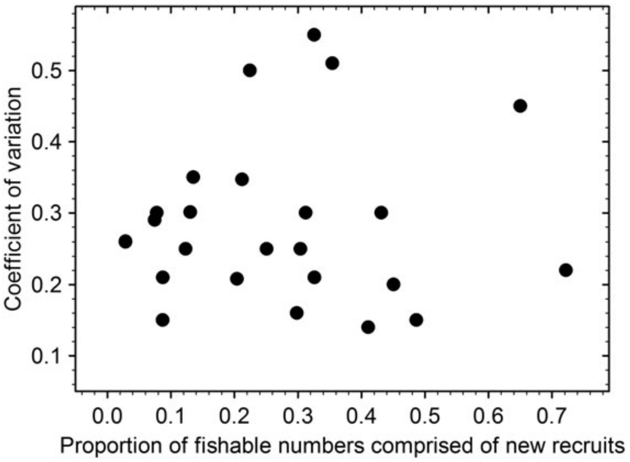

Figure 4. Precision of estimates of the newly recruited year class (represented by the CV of the estimate) as a function of the proportion that year class comprises of the fishable stock numbers for the 2012 assessments of 24 stocks for which full age-structured assessments are available from ICES or the United States National Marine Fisheries Service. The stocks plotted are listed in the Supplemental Material.

In the interest of motivating readers to think about what all of this means, we consider three possible hypotheses to explain this historical trend then go on to present some of the benefits, and costs, of this new reality in fishery science.

Hypothesis 1. All the key research questions about recruitment have been answered.

There is little evidence to support this hypothesis. The 2000s marked the opening of a new millennium, and were accompanied by a number of books and papers intended to lay out the future direction of fisheries and marine science, all trying to sound as forward-looking and innovative as possible (Table 2). Tellingly, none of the quotations, nor the documents from which they were drawn, concludes that the "recruitment question" originally posed by Hjort (1914) has been answered. Rather, in some form or another, each imbeds the still-unanswered questions about the drivers of recruitment variability into even larger and more complex questions. For example, the ICES Strategic Plan (2002) aims to "describe, understand, and quantify the state and variability of the marine environment in terms of its physical, chemical, and biological processes", to "Understand and quantify the role of climate variability and its implications for marine ecosystems" and to "Increase knowledge

Table 2. Extracts from either strategic documents of marine science organizations or government departments, or from "Centennial books" prepared to lay out the future for marine science in the 21st century.

Authors and source	Quotation
R.J. Beamish and B.J. Rothschild. The Future of Fisheries Science in North American. Springer 2009	"The common thread that related all the problems is the basic *understanding of single-species population dynamics* in a multi-species setting involving physical forcing". (p. 9)
ICES Strategic Plan 2002	Describe, understand, and quantify the state and variability of the marine environment in terms of its physical, chemical, and biological processes; (i) Understand and quantify the role of climate variability and its implications for marine ecosystems. (ii) *Increase knowledge of the life history*, stock structure, *dynamics*, and trophic relationships of living marine resources.
40 Priority Research Questions For Ocean Science In Canada A Priority-Setting Exercise by the Core Group on Ocean Science in Canada—Council of Canadian Academies	Although the entire report avoids the term "recruitment", understanding recruitment variation underlies priority research questions: 11, 12, 13, 15, 16, and 17, and is relevant to questions 1, 3, 7, 28, and 29.
EU Marine Board: Science dimensions of an Ecosystem Approach to Management of Biotic Ocean Resources (SEAMBOR) Marine Board-ESF Position Paper 14	Priority gaps for an ecosystem approach are: (i) Understanding the dynamics and resilience of populations, communities and ecosystems. (ii) Scales of variation in ecosystem state and function—over what time and space scales do ecosystems vary and by how much? What are the critical natural factors and processes which determine ecosystem function and state? (iii) Processes of ecosystem change—when ecological change is large and difficult to reverse. (iv) Interconnected ecosystems and their dynamics, the importance of complexity and diversity in maintaining healthy seas.

Extracts are direct quotations of whatever strategic goal(s) or research theme(s) was considered to include work that would have been recognized in earlier decades as "recruitment research".

of the life history, stock structure, dynamics, and trophic relationships of living marine resources" without ever mentioning recruitment in the key activities (see Table 2). Several avoid the word "recruitment" altogether, while proceeding to describe parts or all of exactly the work that Hjort (1914) brought into focus regarding how environmental drivers, biotic interactions, and exploitation affected the dynamics of the large fish stocks of the North Atlantic. This indicates that recruitment questions may be falling out of favour, at least if posed as questions about recruitment variability *per se*. However, we perceive that the processes and relationships of interest to Hjort remain key research questions today, they are simply packaged using different jargon.

Hypothesis 2. The volume of research on recruitment processes has declined because the answers are no longer relevant.

There is little evidence to support this hypothesis. Neither the relevance of recruitment to strategic research planning discussed above nor our review of two dozen flagship stocks from northwest Europe and the United States, supports this hypothesis. With the great emphasis on fisheries advice documented with Indicator 2 (Supplementary Tables S2 and S3), new recruits commonly comprise a substantial part (at least 20%) of the fishable stock (Figure 4) and their numbers are known less accurately than the numbers of older age classes (Figure 4). This leads us to conclude that the abundance of recruits still matters to the harvest of many important fish stocks and is, in fact, one of the more uncertain estimates in the annual assessments of stock status. Analytical methods used in developing harvest advice can manage the risk associated with this greater uncertainty in incoming recruitment, but at a high cost in forgone harvest (Engan *et al.*, 1997; Winemiller, 2005). However, these results are inconsistent with the hypothesis that recruitment research is decreasing because recruitment estimates no longer matter in assessment or management.

Hypothesis 3. Recruitment research has been co-opted by more trendy, possibly ephemeral, research topics.

We consider this a plausible hypothesis, for the following reasons. The word "recruitment" is notably absent from the strategic goals and research priorities being proposed by leading thinkers, agencies, and institutes involved in fisheries science (Table 2). Nevertheless, almost every description of research on how climate change may impact marine ecosystems (e.g. Blanchard *et al.*, 2012; Hollowed *et al.*, 2013), or what factors should be considered under EBFM (Francis *et al.*, 2007; Rice, 2011) or integrated assessments (see Link and Browman, 2014 and articles cited therein) focuses on the parameters of population productivity—recruitment, growth, and natural mortality. Moreover, of these three parameters, interannual variability in recruitment continues to be greater, often *much* greater, than interannual variability in the other two factors. From this we conclude that the "recruitment problem"' has not gone away. Rather, it appears to have been stealthily subsumed by new terminologies, although possibly not with a very different agenda.

In our view, the core question that stems from the preceding is whether this new terminology/repackaging brings with it new and fresh thinking. If so, then the repackaging may be providing substantial benefits. If not, there may be costs. We take this question up in the remainder of this paper.

Possible benefits of repackaging the "recruitment problem"

Some potential benefits of repackaging recruitment research as a subset of EBFM or climate change impacts are as follows:

(i) Conferring more immediacy and a broader applied context. This might bring the results of recruitment research into practice in policy and management faster, rather than leaving the results as just greater academic knowledge that has to then be brought into policy and management by some other avenue. Rendering the research more immediate also plays into the race for "impact", such as more citations to articles within the first 2 years following publication (and, therefore, a higher journal impact factor) and media coverage.

(ii) Embedding recruitment research into a broader applied question might allow the research community to ask at what point is enough understood about recruitment variation so that research into other areas of uncertainty could be prioritized. This is because the processes determining recruitment are complex and, therefore, research into these processes has sometimes got lost in the details of that complexity with a resultant loss of focus on the bigger picture.

(iii) Encouraging broader and more imaginative thinking. New ways of looking at old problems can sometimes shed new light on factors that had been impeding progress.

All these are attractive benefits, *if* they are actually happening—readers can decide for themselves if they are.

Possible costs of repackaging the "recruitment problem"

The potential costs of repackaging recruitment research include the following:

(i) Tying recruitment research to one specific use of the knowledge and one specific aspect of "understanding". While this might allow fisheries management to improve in a particular way, the applied path may not provide any general insight into what causes variation in recruitment. Nesting explanations of recruitment variation in the specific context of fisheries management may make it harder to apply the knowledge of recruitment processes to other policy and management contexts, such as conservation of inherently rare species or habitat restoration.

(ii) Placing recruitment research in competition with other "ecosystem aspects" of the same stock and fishery, or other aspects of research on climate–ocean interactions, may encourage research teams to work on simpler processes for which answers may be easier and quicker to obtain, leaving questions about recruitment variability unexplored despite their greater importance to stock or ecosystem dynamics.

(iii) Removing the incentive and context for looking at broad process-based answers in favour of mechanical descriptions of the pattern in environmental drivers of stock dynamics, whether in the context of climate or fisheries pressures. Researchers may be satisfied with superficial relationships that have some short-term (and possibly ephemeral) predictive power, and not give the relationships the scrutiny that they would receive in a process-oriented study of recruitment.

(iv) Distancing "modern" research from "old" concepts of recruitment will, over time, isolate us from the rich history of recruitment research. Because good researchers have worked on "the recruitment problem" for decades, and found the problem complex but tractable (at least in pieces), many important lessons have been learned. There is no certainty that those lessons will be transferred to research on EBFM or climate–ocean interactions, particularly if the specific term "recruitment" is being avoided.

(v) Some have argued that "the recruitment question" is simply too difficult because too many physical, chemical, and biological factors affect recruitment and the weights of the specific drivers in determining year-class strength may be quite different from year to year (e.g. Suda *et al.*, 2005; Zhang *et al.*, 2010). While this complexity is real, subsuming recruitment research within EBFM or climate–oceans research does not make the natural science aspects of the recruitment problem suddenly easier. Rather, the already complex recruitment problem becomes a part of even larger and more complex problems. It seems difficult to argue that making a hard problem even harder makes it easier to solve.

(vi) EBFM and climate change adaptation research have strong socio-economic components (Miller *et al.*, 2010; Charles, 2012). Embedding recruitment research into these broader questions adds new dimensions of complexity to the research environment, as well as making the natural science dimension even more complex.

(vii) Following from the last three points, historically, recruitment research was embedded in a strong scientific culture, with many researchers more interested in increasing knowledge than in being directly involved in fisheries policy. This may have accorded recruitment research some protection from partisan politicization. Both EBFM and climate change research occur in politicized contexts with much shorter histories—therefore, they may not have as effective a culture of independent science, even if the scientific community strives for it. Bringing recruitment research into these highly politicized decision-making contexts adds new political challenges while removing few if any of the previous ones.

The list of potential benefits of making recruitment research a subsidiary of some greater research questions is short and, in our view, does not overcome many and basic drawbacks.

A large fraction of the questions central to EBFM and climate change research are about how various drivers affect, and are affected by, recruitment variation. Calling research on such questions "recruitment research" would not make the results any less available for uptake by managers and policy makers, but would place the results in a larger historical context than if they were presented as a minor part of some larger EBFM or climate-related research programme.

If the trends that we identify here continue, we will be allowing a key unanswered question in aquatic population and community dynamics to fade away before it was answered or demonstrated to be unworthy of further attention. Recruitment variation still matters, for all the reasons that prompted John Hjort to undertake the work that made him a great leader of marine science, during his time and thereafter (Rozwadowski, 2002; Aksnes and Browman, 2014; Hubbard, 2014; Schwach, 2014). Research into the drivers of recruitment variability is directly relevant to ecosystem-based fisheries policy and management, and to developing adaptation strategies in the face of climate change. Reducing and/or disguising research on recruitment is not a great precedent to be setting at any time, and particularly not on the centenary of Hjort's seminal treatise. We should not be turning our back on his legacy—studying recruitment variability is as relevant today as it was 100 years ago.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We are grateful to Dag W. Aksnes for the citation data to Hjort (1914) upon which Figure 1 is based, Steve Shema for his work data mining the recruitment literature, and Caroline Durif for the help in drafting the figures. H.I.B.'s contribution to this article was supported by Project # 83741 ("Scientific publishing and editing") from the Institute of Marine Research, Norway.

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ICES Journal of
Marine Science

ICES International Council for the Exploration of the Sea
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ICES Journal of Marine Science (2014), 71(8), 2300–2306. doi:10.1093/icesjms/fst215

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Food for Thought

Hazard warning: model misuse ahead

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Dickey-Collas, M., Payne, M. R., Trenkel, V. M., and Nash, R. D. M. Hazard warning: model misuse ahead. – ICES Journal of Marine Science, 71: 2300–2306.

Received 30 May 2013; accepted 14 November 2013; advance access publication 9 January 2014.

The use of modelling approaches in marine science, and in particular fisheries science, is explored. We highlight that the choice of model used for an analysis should account for the question being posed or the context of the management problem. We examine a model-classification scheme based on Richard Levins' 1966 work suggesting that models can only achieve two of three desirable model attributes: realism, precision, and generality. Model creation, therefore, requires trading-off of one of these attributes in favour of the other two: however, this is often in conflict with the desires of end-users (i.e. mangers or policy developers). The combination of attributes leads to models that are considered to have empirical, mechanistic, or analytical characteristics, but not a combination of them. In fisheries science, many examples can be found of models with these characteristics. However, we suggest that models or techniques are often employed without consideration of their limitations, such as projecting into unknown space without generalism, or fitting empirical models and inferring causality. We suggest that the idea of trade-offs and limitations in modelling be considered as an essential first step in assessing the utility of a model in the context of knowledge for decision-making in management.

Keywords: climate, fisheries, GAM, management, prediction, projection, recruitment, time-series analysis.

Introduction

Models are a key tool to build understanding and provide insight in our exploration of the marine ecosystem. The ambition to gain understanding is in part stimulated by our inherent curiosity and in part by our societies' need to manage human impacts. Hjort (1914) typified both of these ambitions; the urge to improve scientific understanding and the need to understand the dynamics of fish stocks to improve the yield of fisheries. A century later, we are still being challenged to understand the "drivers" of marine productivity and thereby inform the management of human impact and ensure both sustainable exploitation and conservation of our seas and oceans. Models can provide the information base for the ecosystem dynamics and human activities and also inform us about the likely consequences of our actions.

In their influential article, Walters and Collie (1988) argued that the evidence base in fisheries was not being fully utilized as a result of an over-reliance on correlative and biological process studies. They dwelt on the impact of spurious correlations that misdirect research and suggested that a lack of experimental control confounds our research, especially when basic statistical precautions are ignored. Myers (1998) continued the theme, showing that most reported correlations between recruitment and environmental explanatory variables did not hold once retested on a longer time-series. Similarly, Ulltang (1998) highlighted the drift away from incorporating biological knowledge into stock assessments in favour of a focus that is solely statistical in its nature. We felt motivated to write this manuscript as we feel that despite the warnings of Walters and Collie (1988), Myers (1998), and Ulltang (1998), much of the marine science community still seems to assume that a correlative relationship provides evidence for causality, which can then be used in advising management. This principle of "covariance over time demonstrates causality and thus can inform management" is being used to push inappropriate modelling approaches to increase our scientific understanding and inform management. Such an approach is clearly flawed: taken to its extreme, it would encourage the widespread consumption of chocolate to increase society's cognitive powers (Messerli, 2012; Figure 1). The central issue, however, is not that the over-reliance on correlative analysis is bad practice, but that models should be appropriate for the question that is being posed.

The question of scale, for example, is central to the appropriate application of a model (Hastings, 2010). All processes can be considered linear over a sufficiently small scale, i.e. any non-linear function can be approximated by piecewise linear regression (Seber and Wild, 2003). However, beyond that characteristic scale, deviations from linearity start to become important and must be considered in the core structure of the model. This property will be further compounded when the dynamics of the system occur at broader scales than that for which we have data (Levin, 1992), e.g. short time-series, or when proposing to project beyond the known range of states (Carpenter, 2002). However, both scientific curiosity and management applications often require extrapolation beyond the known space (such as new regimes or different scales). Obvious examples of this in the fisheries context are the projection of stock recoveries, future recruitment in new regimes, losses due to predator–prey interactions and exploring future climate scenarios.

Importantly, modelling for knowledge building is often substantially different from modelling for management advice (Levin, 1992; Starfield, 1997). The former provides information on function alone while the later must provide information for action, based on our understanding of the underlying processes. Thus, the context of the modelling is different, as ideally the model should be considered as an entity within the management framework. This is further explored by Rose and Cowan (2003) who explore six lessons for ecologists from fisheries management.

The use of frameworks, within which models are imbedded, is commonplace in many disciplines. In assessing climate change impacts, vulnerability and adaptation in human populations, for example, Klein and Juhola (2013) adapt previously presented complex "frameworks" into a framework based on a series of clearly identified principal issues and approaches. The modelling is focused specifically on the issues identified at the outset.

In this manuscript, we explore the appropriate choices about the utility of models in various manifestations within a framework for

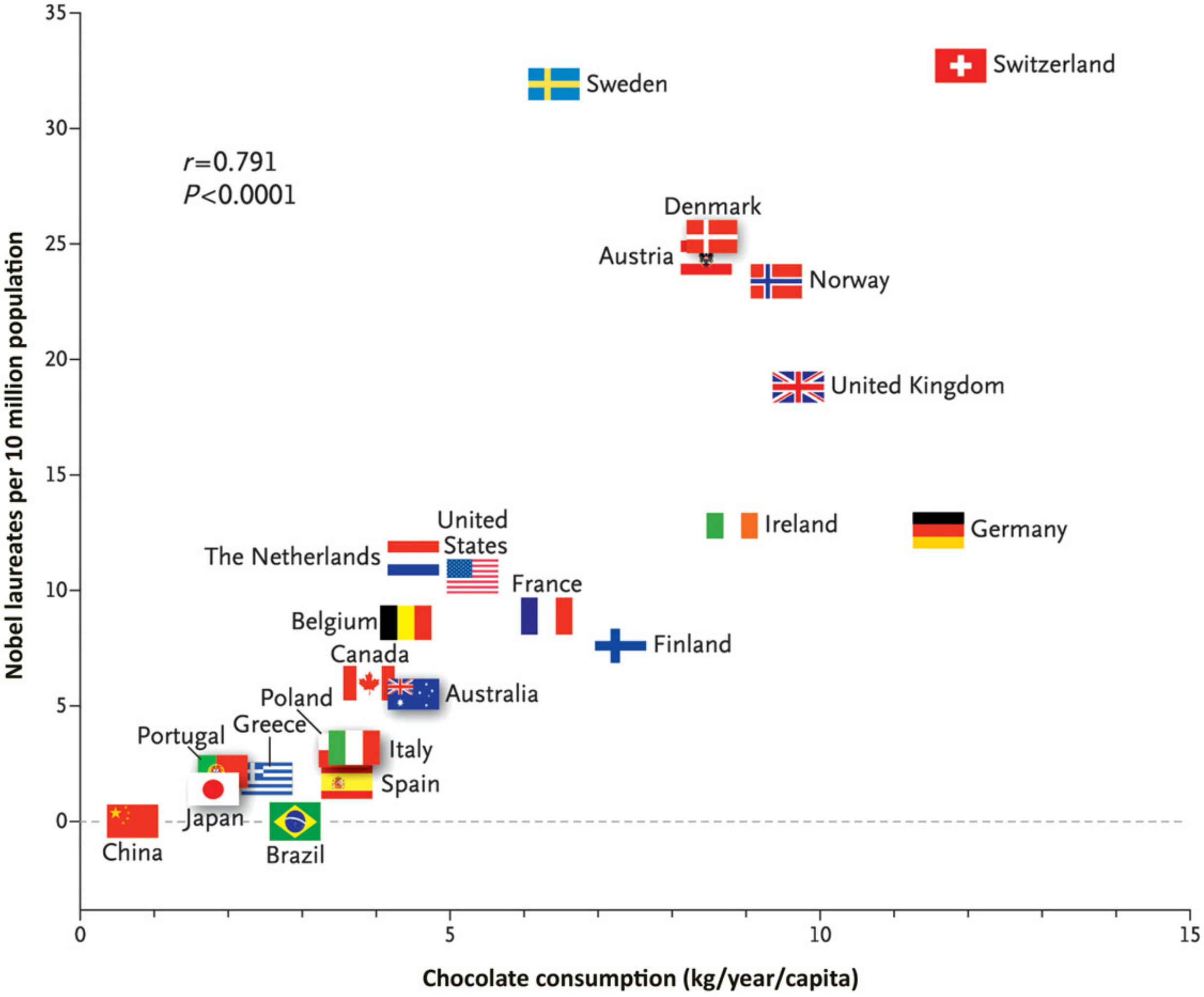

Figure 1. Taken from Messerli (2012). Correlation between countries' annual per capita chocolate consumption and the number of Nobel laureates per 10 million population. Copyright "The New England Journal of Medicine".

providing management advice. We focus primarily on applied marine science and the areas of interest to Johan Hjort. We highlight the traps that commonly ensnare researchers. We propose a framework enabling researchers to consider the nature of the model within the application of the research or management question. We demonstrate this framework with some relevant examples.

Selecting the modelling approach

No model is, or can be, a perfect representation of nature. Models, both in the mathematical and conceptual usage of the word, express the human understanding of the subject under study and thereby reduce complexity to a manageable and accessible form. In the process of creating a model, a reduced fidelity to "truth" is the price paid for simplification. All models are therefore "wrong", to paraphrase Box and Draper (1987), so the question becomes "how useful are they?" This key question, we propose, can only be answered in the context of the application for which the model is intended.

One way to approach the question is by recognizing the existence of the trade-offs inherent in modelling. In the introduction to his 1966 paper, "The Strategy of Model Building in Population Biology", Richard Levins proposed that a model can be characterized in terms of three desiderata: "realism", "precision", and "generality" (Levins, 1966). Generality refers to the ability of the model to represent multiple situations and therefore implicitly includes the ability to extrapolate beyond the domain in which the model was developed (Levins, 1993). Precision refers to the degree of exactness of the measurements or predictions and incorporates the statistical meaning of the word (spread about the mean; Levins, 1993). Reality refers to the number of underlying processes giving rise to the observations that are incorporated into the model (Sharpe, 1990; Korzukhin *et al.*, 1996). Levins further proposed that any given model can only maximize two of these three attributes. Model formulation therefore includes a trade-off of one of these attributes in favour of the other two.

These trade-offs can be used as the basis of a trichotomous model classification system (Levins, 1966; Guisan and Zimmermann, 2000). The "empirical" models (Type I) focus on statistical descriptions of relationships in a precise and realistic manner, but in doing so sacrifice generality. As Levins notes, "this is the approach . . . of many fishery biologists" (Levins, 1966) and examples include time-series (e.g. Gröger and Fogarty, 2011) and other statistical-based (e.g. Cardinale *et al.*, 2009) approaches to recruitment studies, particularly those incorporating large-scale climatic indices (e.g. Stenseth *et al.*, 2002). The second class of models (Type II) are the so-called "analytical" models, where theoretical processes (the "laws" of science) are expressed and solved in terms of mathematics: such models are by their nature general and make precise predictions, but by their abstracted and simplified nature do not represent the full complexity of reality. Examples from marine science include size-spectra models (e.g. Andersen and Beyer, 2006), Lotka–Volterra predator–prey dynamics (Wangersky, 1978), and analyses based on the optimization of Darwinian fitness (e.g. Visser and Fiksen, 2013). Finally, "mechanistic" models (Type III) are process-based and integrate the individual processes at one scale up to a higher scale: examples include bioenergetic and individual-based models (e.g. Strand *et al.*, 2005), end-to-end models (Rose *et al.*, 2010), oceanographic circulation models and IPCC-class climate models. Such models tend to be general in their nature and contain realistic representations of their systems, but may not necessarily be precise.

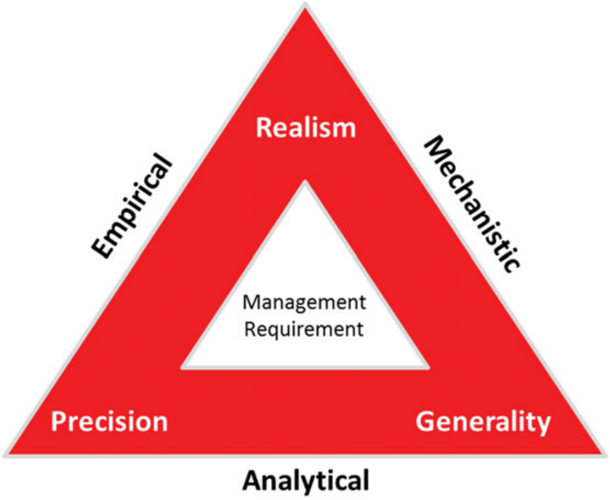

Figure 2. The trichotomous model classification scheme based on Levins (1966) and adapted from Guisan and Zimmermann (2000) and Sharpe (1990). Models are assumed to have two of the three attributes and can be considered empirical, mechanistic, or analytical. Management requirements, however, often lie at the intersection of these attributes, an area which Levins (1966) proposes to be inaccessible.

Based on this trichotomy, the trade-offs inherent in any modelling problem can be visualized in the form of a triangle (Figure 2; Guisan and Zimmermann, 2000). Each vertex of the triangle represents one of the model attributes (realism, precision, generality), and each edge therefore represents one of the model classifications given above. Following the classification of Levins (1966) and Guisan and Zimmermann (2000), model formulations can only exist along the edges of the triangle: the middle of the triangle, where a model combines all three attributes, is inaccessible in the real world. However, it is in this inaccessible area where the expectations of managers often lie.

The Levins trichotomy is particularly attractive in this context as it encapsulates several concepts that we have already touched upon. In particular, causality is closely associated with the generality axis: if the causal mechanisms and processes underlying the question at hand are understood, then generalizing to other situations is possible (Levin, 1992). The mechanistic and analytical classes explicitly incorporate our understanding of causality into their models and therefore use it to achieve generality. In contrast, the empirical models either ignore causal mechanisms or attempt to infer them from correlation: in doing so, they sacrifice generality. Similarly, the use of direct predictors (e.g. food abundance) is common in mechanistic models, whereas indirect predictors (e.g. NAO, AMO, and other large-scale climatic indices) are more common in empirical models.

Levins' work has been highly influential and not without controversy. The paper has been cited more than 580 times (Web of Science, October 2013), including both strong criticisms (Orzack and Sober, 1993; Orzack, 2005, 2012) and robust defences (Levins, 1993; Odenbaugh, 2003) of the work (see references in Orzack, 2012, for a broader overview). Much of this debate has been plagued by semantic differences: Levins did not explicitly define realism, precision, and generality in his original paper, as he believed them to be self-evident [the definitions that we use here are from

Sharpe (1990), Levins (1993), and particularly Guisan and Zimmermann (2000)] but there are also legitimate criticisms of the thesis (see particularly Orzack and Sober, 1993).

Similarly, the model-classification scheme is, of course, imperfect. It can be difficult at times to fit a given model into the classification (Korzukhin *et al.*, 1996). Examples can readily be found that blur the distinctions between the attributes, e.g. the Ricker and Beverton–Holt stock–recruitment relationships have an "analytical" origin (Ricker, 1954; Beverton and Holt, 1957): however, the modern application, especially when modified to include environmental variables (e.g. Mantzouni *et al.*, 2010), is essentially "empirical" in nature. Levins himself, however, did recognize this fluidity (Levins, 1993), describing it as a "delightful" feature, and used it to illustrate that the nature of the model is inseparably linked to its application.

Nevertheless, despite its weaknesses, we assert that the essence of Levins' argument is sound and that it represents a useful way to think about modelling. It is self-evident that no model can be all things to all people. Modelling involves a simplification of the "truth" to make it comprehendible and manageable, and there will naturally arise a bias, conscious or not, towards one aspect of model performance over another (i.e. a trade-off) as a result of this simplification. The important point is that there is a trade-off involved in all modelling. The Levins framework is imperfect and controversial ("wrong"), but, for the sake of the discussions here, we still believe it to be useful.

Creating models

Certain schools in marine fisheries science appear wedded to their techniques and there are fashions in the application of methods and approaches (Johnson and Omland, 2004). This often results in the application of "pet techniques", rather than careful consideration of the appropriate type of model, especially when considering the application to management needs. We argue that the appropriateness of a model is intimately linked to the question that is being posed [a point also stressed by Starfield (1997) for the related field of wildlife management and, as noted above, also by Levins (1993)] and that a model cannot be separated from its intended application. We see three primary applications to which models are put in marine fisheries science:

(i) Knowledge acquisition: the process of trying to understand the characteristics of the system.

(ii) State estimation: attempting to determine the state of the system based on available observations.

(iii) Extrapolation: the use of existing knowledge and/or observations to make statements about scenarios beyond the bounds of the known domain.

It is a combination of 2 and 3 which are used in a management situation, i.e. estimates of the current and predictions of future states of the resource either within or beyond the bounds of the known domain.

Given these types of applications, the Levins trichotomy can be used to identify the model class that should be used to answer these questions. As an example, we consider how the data available to a fish-stock assessment working group could be analysed. If the task was the evaluation of the abundance of a fish stock (e.g. for the generation of management advice), this is a state estimation problem, where accuracy and precision are more important than generality: an empirical model (e.g. time-series model) would therefore be appropriate. However, an analysis of the same dataset to infer the processes influencing recruitment (a classic knowledge acquisition exercise) places value on realism and generality and therefore requires a mechanistic modelling approach. Alternatively, questions about the long-term impacts of climate change (e.g. under various warming scenarios) involve an extrapolation beyond the known range of conditions, and therefore, generality is critical: in this case, mechanistic or analytical models are the most appropriate. The choice of model is therefore determined, in the first instance, by the question that is being posed and not by the datasets or modelling platforms available. System structure and data availability come in the second instance.

As the model and the application need to be considered together, a model can therefore only be judged in the context of its application (Sharpe, 1990; Levins, 1993; Starfield, 1997; Guisan and Zimmermann, 2000). Applying a model in a context outside for which it was designed ultimately risks a mismatch between the (fixed) trade-offs incorporated in the model, and the (shifted) application to which it is put (Levin, 1992). Such mismatches may be the result of a series of active decisions ("mission creep"), or alternatively, they may result from poor model formulation in the first place. In both cases, the outcome is the same: degraded model performance and potentially erroneous conclusions and management advice.

Using models

Unfortunately, the modern application and use of models in applied marine science often does not reflect the pragmatism and common sense encapsulated by Levins (1966). Problems can be identified in both the expectations of the end-users, and the results delivered by the scientific community.

The basic precept of the Levins trichotomy is that the centre of the triangle (Figure 2), where precision, reality, and generality are maximized, is inaccessible. Requests for scientific advice about management options, however, often assume that scientists can deliver all three characteristics; a typical example might be recruitment projections or future distributions and interactions of fish under climate change that could be used to inform harvest strategies. Such expectations are, according to Levins, unrealistic. Of course, the expectations of managers can be made more realistic through a constructive dialogue and iterative process of developing the applied science questions. Many of us though are finding that the work load of managers is too great or that the turnover of managers is too fast to build a constructive working conversation.

The scientific community, however, all too often overlooks the limitations of its work in satisfying such requests. For example, "data mining", with its mantra of "let the data speak" and where the results lead to *post hoc* hypotheses generation, is a classic example of the answer shaping the question. Such empirically derived models are often then used to project outside the known space, as in climate scenarios or projections of recruitment dynamics. Similarly, where two species co-vary in abundance over time, researchers often assume some causal mechanism or some interaction (e.g. sardine and anchovy off California or cod and herring abundance). This simplistic conclusion is often undermined, or at least made more complex when a longer or different time frame is considered or mechanistic or analytical approaches explore the space (Barange *et al.*, 2009; Finney *et al.*, 2010; Speirs *et al.*, 2010; Denderen and Kooten, in press; Hosack *et al.*, 2013). Medium-term (5–10 years) fisheries advice is offered, accounting for interacting species and fleet dynamics, based on the empirically assessed trends in the recent past. This is although human behaviour changes and often finds novel solutions to management restrictions (Rijnsdorp *et al*., 2008; Fulton *et al*., 2011). Recruitment strength can also change rapidly.

There are many challenges when trying to interpret time-series analyses, especially when considering the implications for management action. We feel that this is not strengthened by the *post hoc* use of time-lags, and a failure to consider the appropriate length of the series in relation to the frequency of the signal. Similarly, some theoretical concepts, which have not or cannot be rigorously tested through empirical hypothesis testing (e.g. fisheries-induced evolution, balanced fishing, etc.), have been concluded by induction for specific fisheries without regard to the generality of the approaches.

Furthermore, the willingness to deliver and the unquestioning usage of "pet models" not only leads to inappropriate model choice, but often results in researchers ignoring the particular system structure as well as properties of the data or model parameters. Where some of this comes to the forefront is a researcher with a favoured suite of models or a specific modelling approach that searches for datasets and applies the favoured methodology without due consideration for the question, system and data structure, properties, or implications of the model fits.

Taking heed of some best practice rules and approaches should help to avoid at least some of the pitfalls associated with using models. When fitting empirical statistical models, a basic issue is to ensure that the assumptions underlying the subsequent model fitting are not violated and hence inference can be drawn; carrying out model fitting and selection at the same time causes problems for inference (Chatfield, 1995). A major concern with implementing analytical and mechanistic models is model validation or determination of model skill. Generally, there is no model selection, and thus inference, on process structure (other than via parameter values), though there are exceptions (e.g. Sugihara *et al*., 2012). Ecological inference (or biological inference), i.e. deriving knowledge regarding processes that occurred in the past, based on model selection or comparison is subject to a number of statistical pitfalls. Structure in process errors, such as autocorrelation in space and time will degrade the power of statistical tests, as will structure in measurement (observation) errors. A well-known but often neglected aspect is the measurement error in explanatory variables of regression-type methods—the "errors-in-x" problem (Davies and Hutton, 1975). For example, errors in spawning stock estimates can go as far as masking stock–recruit relationships if they are not accounted for appropriately (Walters and Ludwig, 1981).

Discussion

We propose that the appropriateness of the modelling approach be considered as a first step in the assessment of the utility of models in the context of knowledge for decision making in management. In ICES, the only quality standards for the application of models in management are the peer review process and the lack of strong opposition (rather than consensus). Resources and attention are limited, and this leads to many models being applied inappropriately: fisheries science, however, is not alone in making this mistake, e.g. wildlife management (Starfield, 1997). Society has chosen that fisheries be managed using evidence-based policies. Pragmatic choices, such as selecting a model that is appropriate for the question, are part of the trade-off required to provide advice in an operational manner.

However, we feel that the drive to reanalyse existing datasets (without new data collection or new process investigations) and the widespread ease of use of statistics packages, without sufficient conceptual understanding, is pushing fisheries science into some very uncomfortable corners. In the fisheries science community, the ability to apply state-of-the-art analytical techniques is often seen as a greater skill than investigating ecological or population dynamics (Orr, 1996; Rose, 1997). The use of advanced statistics does not circumvent the basic fact that linear covariation (correlation) does not necessarily equal causality. Often the models applied have many underlying constraints that, when used by the unwary, are readily violated. There is, unfortunately, insufficient education of marine scientists in statistical techniques or alternately, there is insufficient collaboration between well-trained and knowledgeable statisticians and ecologists. The drive of certain schools to push their "pet" model also reduces the space for considering the appropriateness of model choice and application. Hjort himself was not totally above this tendency as he was a proponent of the newly implemented sigmoidal relationship (Hardy, 1950). Looking beyond fisheries science, the increasing analysis of human activities leading to pressures that impact the state of the marine environment and the linearity assumptions associated with certain integrated ecosystem assessment approaches (Samhouri *et al*., 2010; Jennings and Le Quesne, 2012) pose similar challenges and place further demands for knowledge of the research community.

Hjort was very much a practical scientist working with the fishing industry to open up new fishing grounds and concerned about the welfare of fishers (Hardy, 1950). In addition, he applied methods for population statistics applicable for accident insurance for fishers to fish stocks and his seminal paper (Hjort, 1914) identified relationships between abundances and environmental factors along with structural aspects of the populations (intraspecific factors). Statistics at this time was in its infancy and therefore many of the tools that we take for granted today [e.g. Student's *t*-test (1908), ANOVA (1920)] were simply not available. Instead, Hjort dealt primarily with "conceptual models" which formed the basis of deductions. In a subsequent paper (Hjort, 1926), he revisited his "model predictions" and "tested the theories" that he put forward in 1914 by observing what did occur. It was only later that modern statistical techniques and models could be utilized to mathematically "model" relationships between stock metrics and drivers of change in the stock. Thus, there has been a significant paradigm shift in the way that stock fluctuations are predicted: we doubt, for example, that Hjort would have countenanced the projection of fish catches 50–100 years in the future as a way to inform current decision-making. Within the framework of the Levins trichotomy, Hjort's work was essentially conceptualising empirical knowledge. In the absence of a mathematical basis, his work tended to search for mechanistic understanding by using the support of empirical evidence. The objective was to derive some semblance of realism in short-term projections.

Since Hjort (1914), the fish stocks of the world have been heavily exploited. In addition, there is clear evidence that the environment is undergoing a rapid change due to anthropogenic impacts, i.e. climate change, coastal reclamation and construction, etc. Rather than considering variability in future catches alone, as in Hjort's time, we must now consider the wider stewardship of the marine system, and we must acknowledge that the system is always in flux and that ecosystems regularly change. Also, rather than documenting the change in populations and simply understanding the dynamics the emphasis now is on models which have the ability to encapsulate the current knowledge of the principal drivers of fish stock dynamics and the prediction of short (years to decades) and long-term (century) trends in abundance.

In this article, we provide a warning that often a sense of realism about the limitations of our work needs to prevail. Some could say that we are just stating the obvious, or just regurgitating the process for good scientific practice. However, in our opinion, there are too many examples of the misuse of models which claim to provide information to inform management decisions. The message therefore needs to be repeated: the structure of a model must take its application and utilization into account and the model must be fitted using best practice methods (by this we definitely do not mean easiest or most familiar methods). Conversely, a model cannot be separated from its intended application. We have not highlighted a "hall of shame" by identifying specific studies but instead urge the research community to take a step back from their technique-driven approaches to problem solving and ask themselves what is the research question or management problem and what is the most appropriate way to address the challenge. We have not in this "food for thought" moved into the discussion of using multiple models, as widely advocated in multidisciplinary fields such as climate analysis. However, we would encourage all to look at the developments stemming from Schneider and Dickinson (1974) when they encouraged researchers to think across methods. As alluded to above, managers expect that the scientific community can deliver models that are realistic, precise, and general. The onus therefore lies on scientists to be honest about the limitations of our models and thereby ensure that the expectations of managers are pragmatic and not utopian. Clearly dialogue between policy developers, scientists, and stakeholders is needed when shaping research questions. Our management challenges are far more complex than those raised a century ago and require far more sophisticated analytical tools. In Hjort's time, they used the available tools wisely and within their limits: can the same be said of the present? The lessons of Hjort's work therefore mirror the implicit message of Levins: that we must put the focus on the research question and its context first and consider the data or knowledge base available to answer that question, and the tools to be used in doing so, second.

Acknowledgements

We thank the handling editor, our reviewers, and Nigel Yoccoz for their comments which led to a greatly improved manuscript.

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Handling editor: Gary Griffith

ICES Journal of
Marine Science

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CIEM
International Council for
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l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2307–2322. doi:10.1093/icesjms/fsu148

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Quo Vadimus

Modelling and forecasting stock–recruitment: current and future perspectives

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Subbey, S., Devine, J. A., Schaarschmidt, U., and Nash, Richard D.M. Modelling and forecasting stock–recruitment: current and future perspectives. – ICES Journal of Marine Science, 71: 2307–2322.

Received 29 November 2014; revised 10 August 2014; accepted 11 August 2014; advance access publication 4 September 2014.

This paper presents a brief review of the present state of knowledge in stock–recruitment forecasting, including process and current methodological challenges to predicting stock–recruitment. The discussion covers the apparent inability of models to accurately forecast recruitment even when environmental covariates are included as explanatory variables. The review shows that despite the incremental success in the past hundred years, substantial challenges remain if the process of modelling and forecasting stock–recruitment is to become relevant to fisheries science and management in the next 100 years.

Keywords: environment, forecasting, modelling, review, stock–recruitment.

Introduction

Recruitment is the result of many factors that affect survival from the egg-stage (including parental effects) through to when individuals recruit to the fishery or stock, i.e. a stepwise process through parent, egg, larva, juvenile, and back to adults, where abundance at one stage is a function of abundance at a previous stage (Paulik, 1973; Rothschild, 1986; Ulltang, 1996). The state of a population in any given year is a function of the stock (e.g. reproduction and growth) and recruitment, which is itself a function of past events (e.g. state of the stock, environmental conditions). Recruitment is therefore explicitly linked not only to the amount of spawning-stock biomass (SSB), which is often used as a proxy for reproductive potential or egg production, but also parental size, growth history, and environment of the individual.

When providing strategic, rather than operational advice, it is clear that greater knowledge is required about the variability and trends in fish recruitment. This is because operational advice, in the strictest sense, is concerned with the ground-level approaches of putting management plans into action. Therefore, it tends to be short-term focused, and requires information over a short period, e.g. whether stock levels have decreased, increased, or remained level since last assessment. Strategic advice, on the other hand, tends to be for the long haul (e.g. stock rebuilding plans, maintenance of stock levels) and covers the "what" and "why" of fisheries management decisions. Such decisions will require knowledge of the variability and trends in recruitment, to evaluate the possible effects of management decisions on stock trend variability and to assess the efficacy of decisions in meeting long-term goals.

The issue of recruitment forecasting (for strategic and operational advice) has been a focus for fisheries research over the last hundred years. Unfortunately, it is often now dismissed as an unreachable goal because of the various mechanisms interacting to influence dynamics throughout the life of an individual. Many of these mechanistic links are either poorly known or the link with recruitment holds for only a short period (Myers, 1998), during which the strength can be intermittently strong/weak. Attempts to understand and forecast outcomes, e.g. survival and recruitment, are now in progress through the use of complex and sophisticated individual-based modelling techniques (Peck and Hufnagl, 2012). However, these models still rely on a basic recognition and understanding of the key drivers and mechanisms which influence survival through all prerecruit life stages.

Here we present a brief review of the present state of knowledge in stock to recruitment modelling and forecasting, including methodological challenges to predicting recruitment and potentially its linkages with the parent stock. We discuss several reasons for the current apparent inability to forecast recruitment accurately, especially when environmental covariates are included as explanatory variables. The main questions we ask are (i) what are the influences on recruitment? (ii) do we need to understand the factors influencing each life stage to predict recruitment?, and (iii) do we have the necessary tools to model recruitment? Finally, we examine preconditions necessary for stock–recruitment modelling and forecasting to be recognized as relevant to fisheries science and management in the next 100 years.

Biological mechanism and recruitment drivers

The construct of stock to recruitment is a method of predicting recruitment levels from a known stock size. For various reasons, the SSB is taken as a proxy for the total egg production or stock reproductive potential (see Trippel, 1999). By using stock size and recruitment in a single model, it was implicit that the parent stock size had an influence on the numbers of young surviving to join the parent stock or fishery (Ricker, 1954; Beverton and Holt, 1957). At low stock sizes, recruitment is primarily driven by density-independent factors and thus recruitment increases monotonically with stock size. However, at large stock sizes, other factors, e.g. density-dependent effects (to varying degrees) are more influential on the survivorship of young. This method of estimating recruitment levels into the future is primarily for the purpose of modelling and is not really designed for understanding early life-history dynamics. The necessity to derive such relationships is driven essentially by stock assessment and management needs, such as accurately quantifying the exploitable segment of the population and sustainable stewardship of fisheries resources. It also provides a method of closing the loop in fish population modelling whereby generational input of young fish (new year classes) can be estimated.

A shift in the linkage between SSB and egg production can occur through interannual variations in individual fecundity (McBride *et al.*, 2013), non-participation in spawning by part of the mature population, i.e. skipped spawning (Rideout and Tomkiewicz, 2011; Skjæraasen *et al.*, 2012), or through viability of offspring due to the structure of the mature population (Marshall *et al.*, 2010) Any of these can lead to the errors-in-variables problem when using SSB as the metric to predict productivity (Rothschild and Fogarty, 1989; Morgan *et al.*, 2011). A stock–recruitment relationship (SRR) that fails to consider other factors or their interactions does not incorporate a large amount of biological realism, which leads to an inability to accurately quantify the true effect of factors influencing recruitment.

Stock–recruit models often fail to adequately show the link between spawners and recruits or the link weakens when new or longer datasets are added (Myers, 1998). Factors not directly a consequence of the spawning stock can impact cohorts within the same stock differently and this lack of consistency is often viewed as a breakdown of the relationship. Hutchinson (2008) surmised that the reason for SRR failure is due to either incorrect assumptions regarding the spawning stock or failure to account for the spatio-temporal scales of factors describing the relationship. Furthermore, changes in population demography (Wright and Trippel, 2009; Fitzhugh *et al.*, 2012) may result in a dissociation between SRR and mechanistic relationships, e.g. Atlantic cod SRR with temperature, the North Atlantic Oscillation (NAO), or dynamics of the North Atlantic Subpolar Gyre (see Ottersen *et al.*, 2010). Many SRRs have the assumption of stationarity and so do not effectively deal with shifts in productivity of the ecosystem or the stock itself (Nash *et al.*, 2009). Moreover, system complexity and non-linear interactions between factors, which act to prevent the observed variable from behaving in an expected way, or mask, mitigate, or intensify specific information types, affect the perceived performance of SRRs.

A number of authors have shown that incorporating community dynamics (e.g. prey to-predator loops, Bakun and Weeks, 2006; cannibalism, Hjermann *et al.*, 2007) was more important than solely using environmental factors for accurate predictions of recruitment. The effect of the NAO in the Barents Sea typically reinforces oceanic responses, causing overall higher water temperatures, but it may be that it is not solely temperature that is responsible for strong year classes; the NAO influences the influx of Atlantic Water, which imports not only warmer water but also food (zooplankton) for juvenile cod (Ottersen *et al.*, 2010). Furthermore, one type of interacting term may not be strongly related to recruitment dynamics until another term is added to the model. This was the case for the Northern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) population, where herring (*Clupea harengus* L.) predation was not strongly correlated with cod survival until the effect of temperature was included (Duplisea and Robert, 2008). Fish live in multispecies communities and the effect of interactions between species, or between fish of different sizes within the same species, should not be overlooked. A reversal in the predator–prey dynamic between Atlantic cod and pelagic fish (e.g. herring, mackerel (*Scomber scombrus*)) appeared to drive cod recruitment in the 1970s and 1980s in the Southern Gulf of St. Lawrence, where, when pelagic fish reached high abundance, they preyed heavily upon the eggs and larvae of cod (Swain and Sinclair, 2000). Another type of trophic dynamic exists in the Barents Sea; good year classes of herring result in high mortality of their prey, capelin (*Malotus villosus*) larvae, which acts to deplete the capelin stock (at a lag), leaving little food for adult cod, which then may, depending on cod stock size, turn cannibalistic, resulting in poor cod recruitment (Hamre, 2003). Cannibalism has also recently been suggested for the North Sea autumn spawning herring population as a consequence of a demographic shift in the abundance of substock abundances and a potential overlap of adults with a part of the larval drift pattern (Corten, 2013).

Early life-history dynamics

Traditional stock–recruitment models use the endpoint (i.e. the number of individuals recruiting to the fishery) of a complex relationship that integrates several processes operating over multiple spatio-temporal scales (Rothschild, 2000), but whether this encompasses enough detail is questionable. Stock–recruitment is not only a function of the stock, but is intrinsically linked to past events that influence growth and mortality, not only of the individual recruiting but also of the parents. Recruitment must decline if there is insufficient spawning biomass, but recruitment will also decline with reduced body size, as fecundity, egg size, and spawning extent is inextricably linked to the fish's growth history and condition (Kjesbu *et al.*, 1996). Any factor changing the demography of the population will impact reproductive potential, and hence recruitment of the stock. This multi-scale complexity then argues for a life-stage approach to stock–recruitment modelling (Rothschild, 2000).

An integrated life cycle approach is one that investigates the importance of different mechanisms acting on various life stages and identifies the critical stages and mechanisms for recruitment (e.g. Nash, 1998, and references therein). By partitioning recruitment relationships into different life stages, scale can be explicitly investigated by examining the numerical variability in the relationship, as well as the interaction between life stages and the environment, and the non-linear dynamics regulating each stage (Rothschild, 2000). This approach has been successfully used to investigate recruitment for several stocks, e.g. North Sea herring (Nash and Dickey-Collas, 2005); Northeast Arctic cod (Mukhina *et al*., 2003); and Barents Sea stocks (Dingsør *et al*., 2007). Paulik (1973) highlights this in his seminal work on predictive SRR whereby the various life stages are taken into account when progressing from stock to eventual recruitment.

Paulik diagrams, in their present form (as initially presented by Nash, 1998), provide a graphical format for indicating where bottlenecks or shifts in survival are occurring in the life cycle. An example of this is shown in North Sea autumn spawning herring (Payne *et al*., 2009), where a major shift in survivorship occurred in the first winter of life. From around 2001 to the present, overwintering survival is considerably less than in previous years. In Paulik's original paper (Paulik, 1973), he assumed there would be recognizable relationships between life-history stanzas that could be modelled. The presentations by Nash (1998), Nash and Dickey-Collas (2005), Payne *et al*. (2009), and Nash and Geffen (2012) indicate that the situation is more complex and relationships between life-history stanzas can vary quite considerably.

The impact on environmental factors may be crucial for the early life stages. The link between environment and early life stage survival has been thoroughly investigated through match–mismatch hypothesis (Cushing, 1982, 1990), critical period hypothesis (Hjort, 1914), ocean stability hypothesis (Lasker, 1981), optimal environmental window (Cury and Roy, 1989), and ocean triad (Bakun, 1998). However, larval abundance alone may not be an adequate predictor of recruitment (Stige *et al*., 2013). Furthermore, the environmental link may be indirect; the gadoid outburst in the North Sea occurred when stock levels were not extremely high, but when environmental conditions were good for the prey of early life-history stages of gadoids, namely the prey abundance, seasonal timing, and mean size (Cushing, 1984; Beaugrand *et al*., 2003). Shifts in productivity or survival through the early life history during different thermal regimes was also indicated by Nash (1998) and Nash and Geffen (2012) in Irish Sea plaice (*Pleuronectes platessa*).

In early life history dynamics, there is a recognition that both density-dependent and independent factors occur, but the relative importance of the two shift through ontogeny (Beverton and Iles, 1992a, b). Both density-dependent and -independent processes are assumed to be occurring within a certain recruitment interval, i.e. the period between spawning and recruitment, and all mortality outside of this interval (i.e. post-recruitment) is considered density independent. This assumption is an oversimplification because the length of the recruitment interval is often not based on an understanding of mechanisms or underlying processes, which is an important consideration when attempting to determine the impact of specific mortality influences (e.g. fisheries) on multiple stages (Brooks and Powers, 2007).

By using multiple stages, both the level and type of mortality on each stage can be allowed to vary before recruitment. The question of whether this matters for the timing of compensatory processes, i.e. whether the timing (early or late) in the stage, has a strong effect on the numbers of recruits. As Brooks and Powers (2007) pointed out, additional mortality from exogenous sources will have a larger impact if occurring later in the stage, after compensatory responses have occurred, regardless of whether the Beverton–Holt or Ricker model is used to investigate recruitment. Various authors have illustrated the differences in mortality rates through the early life-history stages (e.g. Nash and Geffen, 2012) and highlighted the fact that the absolute level of mortality is a function of both the instantaneous rate and the stage-duration.

Modelling stock–recruitment

In the fisheries literature, recruitment models can be classified as being parametric, semi-parametric, or non-parametric. Parametric recruitment models are analytical or semi-analytical functional expressions for recruitment. Three subclasses of parametric approaches to modelling stock–recruitment are identifiable from the fisheries literature, which we classify as classical, Box–Jenkins type, and state-space models. The first subclass includes the two parameters Beverton and Holt (1957) and Ricker (1975); the general recruitment function by Deriso (1980), Cushing (1973), Iles (1994), and Shepherd (1982); and the Sigmoidal Beverton–Holt (Myers and Barrowman, 1995) models. A good summary of the most widely used parametric recruitment models can be found in Needle (2001). Included in this subclass is cases where one of the classical functional relationships (Beverton–Holt or Ricker) is augmented with secondary data (climatic and ecological) such as temperature and prey interactions (see, e.g. Gjøsæter and Bogstad, 1998; Planque and Frédou, 1999; Olsen *et al*., 2011). The second subclass of parametric recruitment functions is those in which the dependent variable (here recruitment) is regressed on one or several (often time-lagged) independent dataseries, including time-lagged values of the independent variable. This subclass of time-series models (also referred to as Box-Jenkins models, Box *et al*., 1994) consider recruitment as a combination of autoregressive and moving average effects, leading to an autoregressive moving average model (see, e.g. Gröger *et al*., 2010; Gröger and Fogarty, 2011). The third subclass involves the use of state-space model formulations to link recruitment to population parameters. In general, discrete-time state-space models are defined by two equations, namely, the observation (or measurement) equation and the system (or transition) equation. This model class, based on linear difference relationships between the input and output variables, provides and offers the additional flexibility of including parameters that are exogenous to the model. An example is the Bayesian state-space stock–recruitment model for Fraser River pink salmon (*Oncorhynchus nerka*) (Meyer and Millar, 1999). The state-space approach addresses two major problems encountered in traditional stock–recruitment analyses that of errors-in-variables bias and time-series bias. In Meyer and Millar (1999), both process and observation errors were explicitly captured in the state-space model and quantified through posterior distributions of the parameters via the Bayesian paradigm.

Semi-parametric and non-parametric methods derive the recruitment relationship based on less stringent assumptions than those implied by the use of parametric approaches. This class of models spans a wide range including modelling the distribution of recruitment as a function of biomass by non-parametric density estimators (Evans and Rice, 1988), locally weighted smoothing functions with non-parametric regression, LOESS smoothers and spline methods (Cook, 1998; Bravington *et al*., 2000; Cadigan, 2013; Munch *et al*., 2005) and neural networks (Chen and Ware, 1999). Extensions of this class of models to include environmental variables has also been reported in the literature (see, e.g. Jacobson and MacCall, 1995).

This manuscript focuses on establishing an SRR outside the stock assessment model, and involves fitting functional relationships to stock–recruit data. The fitting process results in deterministic (expected recruitment) and stochastic (characterized by residuals resulting from the fit) components of recruitment. It must be mentioned, however, that a common practice is to estimate the recruitment relationship within the model used to assess the stock (see, e.g. Maunder and Deriso, 2003; Lee *et al.*, 2012). When recruitment relationships are integrated into assessment models, the annual recruitment is usually decomposed into two components: an average annual recruitment (synonymous to the relationship obtained by an analytical fit to stock–recruit data) and a stochastic component (e.g. residuals from a functional fit). The stochastic component is usually defined by an assumed probability distribution function, and the parameters for the recruitment relationship (the annual average recruitment and parameters of the probability distribution) are usually integrated into the total objective function for the assessment model. The optimized probability distributions are then used to characterize the uncertainties in the annual recruitment, as well as in recruitment projections. The integration of SRRs can be extended to the case where environmental correlation with recruitment or a stock–recruitment model is being considered (Maunder and Starr, 2001; Maunder and Watters, 2003). See Maunder and Deriso (2003) for instance, for several estimation methods involving catch-at-age assessment models with integrated recruitment estimation components.

Functional SRRs

The classical approach to stock recruitment assumes the existence of a functional relationship, $F(\cdot)$, between spawners, S_t, and recruits, R_t, over some indexed time (usually years) of $t = 1,\ldots,n$. This relationship can be expressed in a compact form as

$$R_t \equiv F(S_t, \Theta), \qquad (1)$$

where Θ is a vector of parameters, usually of direct relevance to the fishery management policy (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Chen, 2004).

Deriso (1980) introduced the general three-parameter SRR in (2), which was further developed by Schnute (1985). The resulting Deriso–Schnute model,

$$R_t = \alpha S_t (1 - \gamma \beta S_t)^{1/\gamma}, \qquad (2)$$

is such that

$$R_t = \begin{cases} S_t e^{\alpha - \beta S_t}, & \lim \gamma \to 0 \\ \dfrac{\alpha S_t}{1 + \beta S_t}, & \gamma = -1. \end{cases} \qquad (3)$$

The models resulting from setting $\lim \gamma \to 0$ and $\gamma = -1$ define, respectively, the Ricker (1975) and the Beverton and Holt (1957) models, which are the most commonly used stock–recruitment models in fisheries science. The parameter α is the density-independent parameter, and β measures the level of density-dependence. The shape parameter γ is, however, not limited to $\gamma \leq 0$. For instance, $\gamma = 1$ leads to the Schaefer model (Schnute, 1985; Schaefer, 1991) for recruitment. Also, note that we can derive the following equation (dropping the time subscript) from (2):

$$\frac{d(R/S)}{dS} = -\frac{\beta}{1 - \beta\gamma S}\left(\frac{R}{S}\right).$$

Hence the compensatory property, $d(R/S)/dS < 0$ is only guaranteed for $\beta(1 - \beta\gamma S) > 0$ for all S. For a comprehensive discussion, see Quinn and Deriso (1999).

The Beverton–Holt and Ricker models both describe a decrease of the per capita recruitment with increasing stock size. Mortality is assumed to be density independent at low stock sizes and there is scope for some underlying level of density-dependent mortality at any stock size. The choice of the stock–recruitment model is based upon the severity of the density-dependent mortality (the existence of "overcompensation") believed to influence population dynamics most during the period before recruitment. The Beverton–Holt model is based on the assumptions that juvenile competition results in a mortality rate that is linearly dependent upon the number of fish alive in the cohort at any time. It also assumes the ever presence of predators. The Beverton–Holt model is appropriate "if there is a maximum abundance imposed by food availability or space, or if the predator can adjust its predatory activity immediately to changes in prey abundance" (Wootton, 1990). The Ricker model is based on the assumption that the mortality rate of the eggs and juveniles is proportional to the initial cohort size. The ecological conditions that result in a Ricker-type recruitment include (i) cannibalism of the juveniles by the adults, (ii) disease transmission, (iii) damage by adults of one another's spawning sites, (iv) density-dependent reductions in growth coupled with size-dependent predation, and (v) a time-lag in the response of a predator or parasite to the abundance of the fish (Ricker, 1975; Wootton, 1990).

At low stock sizes, depensatory effects may occur. The decrease of per capita recruitment is commonly referred to as the Allee effect (Allee *et al.*, 1949). In terms of modelling, the Allee effect is a zero-recruitment term, which represents an offset of the recruitment function from the origin (see Frank and Brickman, 2000). Models incorporating depensatory effects may be three-parameter generalizations of the Ricker (see, e.g. Chen *et al.*, 2002), the Beverton–Holt model (see, e.g. Liermann and Hilborn, 1997), or the Saila–Loda model (Saila *et al.*, 1988).

In the literature, the classical equations (Beverton–Holt and Ricker) have also been reformulated to provide direct information about the productivity and resilience of a fish stock, and hence to management. The reformulation incorporates a parameter, referred to in the literature as *steepness*, and defined as the proportion of virgin recruits produced by 20% of the virgin spawning stock, (see, e.g. Mace *et al.*, 1988; Brooks and Powers, 2007). First, let h, R_0, E_0, ψ_0 represent the steepness, virgin recruitment, virgin egg production, and virgin level of egg production per recruit ($\psi_0 = (E_0/R_0)$), respectively. We denote by $R_i(t)$ the number of fish surviving to time t of stage i $(0 \leq t \leq q\Delta t_i)$, where Δt_i $(i = 1,2,\ldots,n)$ is a unit duration of the recruitment process, assumed to occur over n discrete stages. Then the number of fish at time 0 of stage 1 is the number of eggs produced, i.e. $E \equiv R_1(0)$.

The reparametrized Beverton–Holt and Ricker functions are then defined by

$$R = \begin{cases} \dfrac{4hR_0E}{\psi_0 R_0(1-h) + (5h-1)E}, & \text{Beverton-Holt} \\ \dfrac{E}{\psi_0}(\beta\psi_0)^{(1-E)/E_0}, & \text{Ricker.} \end{cases} \qquad (4)$$

A high steepness value is indicative of a resilient population, which is robust to harvesting, including a high probability of rebuilding when fishing pressure is relaxed. It must be mentioned, however, that despite its attractiveness, the steepness parameter is difficult to estimate because there is often little information in the data on this parameter (Lee *et al.*, 2012).

Incorporation of environmental effects

Demographic uncertainty is the result of inherent temporal variability in population processes due to environmental stochasticity. The goal of including environmental covariates in stock–recruitment modelling is to reduce the degree of unexplained stock–recruitment variation caused (at entry to the fishery) by demographic variation. When building recruitment models, a challenge is the question of whether or how environmental influences should be included in the model definition. The most common models for incorporation of environmental variables $Z_1, \ldots, Z_n$ in SRRs are modified Ricker or Beverton–Holt functions (Hilborn and Walters, 1992; Chen and Irvine, 2001) of the form

$$R_t = S_t e^{\alpha - \beta S_t + c_1 Z_1 + c_2 Z_2 + \cdots + c_n Z_n}, \tag{5}$$

$$R_t = \frac{\alpha S_t}{1 + \beta S_t} e^{c_1 Z_1 + \cdots + c_n Z_n}. \tag{6}$$

Of these two models, the modified Ricker model is the type of relationship more commonly investigated. This is perhaps because similar to a lognormal error; this allows for a linear and additive formulation of the model, thus affording computational ease. This type of model has, for instance, been used by Planque and Frédou (1999) and Drinkwater (2005) to describe recruitment of Irish Sea cod. The effects of predators and competitors of Northwest Atlantic cod have been studied using a linear regression of $\log(R/S)$ against SSB of cod, herring, and mackerel (Swain and Sinclair, 2000). A hybrid Beverton–Holt–Ricker model was used to incorporate zooplankton abundance and a log-linear effect of temperature (Olsen *et al.*, 2011).

Myers (1998) pointed out that environment–recruitment relationships are seldom used in stock assessment. For instance, Shepherd *et al.* (1984) listed 42 stocks in the North Atlantic and Northeast Pacific, for which the environmental impact on recruitment had been studied, but only one correlation had become part of stock assessment. Furthermore, Myers (1998) found that correlations, in general, performed poorly on retesting with longer time series, with exception of relationships at population's geographical limits. The problem of data-dependence on choice of tests for correlations and their results has also been highlighted by Iles and Beverton (1998).

More generally, a major drawback with models of the forms (5) and (6) is that they are usually linear approximations of non-linear environmental effects. This approximation may be inadequate or unreliable. For example, Drinkwater (2005) and Planque and Frédou (1999) found evidence for a non-linear relationship between temperature and recruitment. For cold-water species, warmer sea temperature would strengthen recruitment and for warm-water species, the opposite. However, the actual response was dependent on where in the latitudinal range of the species the observations were made. A quadratic relationship between sea surface temperature (SST) and the logarithm of the reproductive success was reported by Stocker *et al.* (1985). Such a dome-shaped functional relationship cannot be described by a log-linear model such as (5) or (6). The logarithm of a linear function can be a strictly monotonic decreasing or increasing function, but does not allow for both a positive and a negative slope of the environment–recruitment curve. This fact is of special significance, since the rejection of a linear relationship does not necessarily imply the total absence of one, but that the functional form may be non-linear. On the other hand, suppose the influence of an environmental parameter (e.g. temperature), T, on recruitment is defined as the exponential of an n-dimensional polynomial with coefficients $a_0, a_1, \ldots, a_n$, and given by (7)

$$R_t = f(S_t) \exp\left(a_0 + \sum_{j=1}^{n} a_j T^j\right), \tag{7}$$

where $f(S_t)$ is a function of S_t. Then the effect of T on R_t will be not unique, but depend on the values of the coefficients of the polynomial. For the simplest case of $n = 2$ (quadratic polynomial) recruitment can be lower both at low and high temperatures (for fixed values of S_t and T), depending on the values of a_1 and a_2.

It is worth mentioning that functional forms other than log-linear have been suggested by Iles and Beverton (1998). Semi-parametric and non-parametric models incorporating environmental parameters have also been reported in the literature. For instance, Chen and Irvine (2001) used semi-parametric models of the form (8), where $g(E)$ denotes a linear or quadratic function of one or several environmental factors E and $f(S_t)$ is a linear function of S_t.

$$R_t = S_t e^{\alpha + f(S_t) + g(E)}. \tag{8}$$

Fitting stock–recruitment functions

Error assumptions

Although some authors (see, e.g. Jiao *et al.*, 2004) have modelled the SRR assuming normal, lognormal, gamma, and Poisson model errors, the predominant assumption is that the errors in the spawner–recruitment relationship are usually lognormally distributed (Hilborn and Walters, 1992). A stochastic version of the classical Beverton–Holt and Ricker functions, given lognormal errors, can be formulated as

$$R_t \equiv F(S_t, \Theta) e^{\epsilon_t}, \tag{9}$$

where $\epsilon \sim N(0, \sigma^2 I)$. The assumption of lognormal errors in the SR analysis can be attributed to principal contributions by Allen (1973), Walters and Hilborn (1976), Peterman (1978), Hennemuth *et al.* (1980), and Peterman (1981). The basis for the lognormal assumption, however, derives from empirical studies (see, e.g. Allen, 1973; Peterman, 1981) or driven by the need for computational convenience and ease (see, e.g. Hilborn, 1985), or a combination of both factors (Walters and Hilborn, 1976). However, a common practice in fitting the SRR is to first introduce a linearization of the model equation (e.g. by taking the logarithm of R_t, as in Chen, 2004), followed by parameter estimation using a least-squares approach, where the lognormal error assumption provides computational ease.

The literature, however, shows that non-parametric and Box–Jenkins models allow for consideration of other types of error structures other than lognormal (Meyer and Millar, 1999). Generalized linear models (GLMs), which are a flexible generalization of ordinary linear regression, are applicable to several error distributions other than the normal. Jiao *et al.* (2004), for instance, used a GLM to investigate the effect of normal, lognormal, gamma, and Poisson model error assumptions on the derived SRR. Other non-parametric methods in the literature include density estimation

(Evans and Rice, 1988), generalized additive models (Jacobson and MacCall, 1995), locally weighted spline smoothing with non-parametric regression (Cook, 1998), and neural networks (Chen and Ware, 1999). It must be noted that since most non-parametric methods are heavily dependent on asymptotic assumptions, their reliability, when applied to small sample sizes typically available for recruitment series, may be unknown.

Bias and bias correction

In general, the difference between an estimator's average and the true parameter value is called the bias. In stock assessment models, recruitment variability is usually assumed to be lognormally distributed (Maunder and Deriso, 2003). Methot and Taylor (2011) showed that the lognormal assumption calls for a bias correction in the modelled mean annual recruitment. We define the true (but unobserved) and modelled mean annual recruitment values, respectively, by R and R^*, and assume that R^* is lognormally distributed, i.e. $\log(R^*)$ is normally distributed with mean R and standard deviation σ_R. Then the true mean recruitment is considered as a random variable, which is related to the modelled recruitment through

$$R^* = R\exp\left(\left[u\sigma - \frac{1}{2}\sigma^2\right]\right), \qquad (10)$$

where u is a normally distributed random variable with zero mean and unit variance. The term $1/2\sigma^2$ is subtracted to make R^* unbiased, i.e. we have

$$\mathbb{E}(R^*) = R, \quad \mathrm{Var}(\log(R^*)) = \sigma^2. \qquad (11)$$

As stated in Methot and Taylor (2011), the adjusted value $R^* < R$, and represents the median recruitment value.

Formally, an estimator θ^* of a real-valued parameter θ is median-unbiased if

$$\text{Probability } [\theta^*(X) < \theta|\theta] = \text{Probability } [\theta^*(X) > \theta|\theta],$$

for each θ (Birnbaum, 1964), i.e. under- and overestimates are equally likely. On the other hand, θ^* is mean-unbiased if for each θ, the expectation of θ^* is defined such that

$$\text{Expectation } [\theta^*(X)|\theta] = \theta.$$

Both mean-unbiased and median-unbiased estimates of stock–recruitment have been reported in the fisheries literature. Unfortunately, the literature offers no guidelines for which to prefer and why, although the estimators have different attributes and probabilistic expectations. When the estimator of recruitment is to be used as input to different (not all linear) formulae (or models); however, then the median-unbiased estimator is to be preferred (see, e.g. Birnbaum, 1964). On the other hand, if one assumes that the recruitment data errors are normally distributed, then the best unbiased estimator will also be normally distributed. Under such assumption, the median-unbiased and mean-unbiased estimators are mathematically equivalent in any linear regression or multivariate analysis. Median-unbiased estimators are however preferable in situations where the normally distributed error assumption cannot be justified (i.e. asymmetric distributions). This is because the median is then insensitive to skewness and kurtosis (see, e.g. Andrews, 1993; Nelson and Plosser, 1982). Because recruitment data are usually heavy-tailed (represent asymmetric distribution), a median-unbiased recruitment estimate may offer a precautionary and preferable alternative for short-term predictions or if estimates are to be used for computing reference points. Median-unbiased recruitment estimates are also to be considered when these values are input parameters to other submodels or equations.

For the general problem of fitting the SR function, the literature shows that a density-dependent SR relationship is generally assumed to exist (Sakuramoto, 2005). It has also been recognized that because estimates of numbers of spawners and recruits are uncertain, the recruit–spawner output is incomplete unless accompanied by estimates of uncertainty (Ludwig and Walters, 1981a). Some emphasis has therefore been placed on how to correct for bias in estimated parameters Θ, due to data uncertainty (see, e.g. Ludwig and Walters, 1981a; Walters and Ludwig, 1981; Walters, 1985; Chen, 2004). Two potential effects of uncertainty on recruitment have been reported, namely (i) the estimated parameters may be inconsistent due to violation of the independent error assumption, which underlies the regression equation and (ii) the overestimation of the information content of the observation data (Ludwig and Walters, 1981b).

For the classical Beverton–Holt and Ricker models, if the errors are lognormally distributed, then the optimal parameter values obtained by multiple linear regression, $\hat{\Theta}$, and the associated variance, $\hat{\sigma}^2_{\Theta}$, can be easily estimated. The multiple regression approach is, in principle, finding a model that quantifies the expected (average) recruitment for a given stock size. However, this average has been shown to be (in most cases) larger than the modal recruitment (Ricker, 1975; Hilborn, 1985). Consequently, bias is introduced in estimates of Θ, with subsequent bias and uncertainty in management decisions, which are dependent on the parameter estimates. Ludwig and Walters (1981a) developed an elaborate estimation procedure, which is robust both to the limited number of observations that are usually available and to measurement errors. The computational framework relies on an independent assessment of the relative strengths of environmental and measurement variances in providing maximum likelihood estimates of Θ, a measure of uncertainty in Θ and a time series of errors. More recently, Chen (2004) argued that the assumption of lognormal errors in the Ricker and Beverton–Holt models introduces a positive bias into recruitment predictions, which is qualitatively dependent on the structure of the model residual variance, the historical SR data, and the specific spawner biomass used. The bias correction introduced by Chen (2004) is reported to be asymptotically unbiased with a finite-sample bias that is practically zero.

Forecasting stock–recruitment

Recruitment forecasting often involves the use of environmental indices because, often, prerecruit data are either unavailable or highly uncertain. Examples include recruitment forecasting of short-lived species such as anchovy in the Bay of Biscay (*Engraulis encrasicolus* L.), where upwelling conditions caused by north-easterly winds of medium and low intensity in spring–summer in the Bay were linked to good levels of recruitment (De Oliveira *et al.*, 2005), linking SST and recruitment to predict the impact of increasing sea temperatures on future recruitment (Roel *et al.*, 2004), and the use of SST to predict California sardine (*Sardinops sagax*) recruitment (Jacobson and MacCall, 1995). The attempt to predict short-term changes in recruitment of North Sea cod using SST has also been reported by Planque *et al.* (2003). Multiple regression recruitment forecast models have also been developed for

Northeast Arctic cod, Norwegian spawning herring, and Barents Sea capelin. These models combine the water temperature of 3–7 stations of the Kola section transect (layers 0–200 m) (see Bochkov, 1982), the bottom-trawl abundance indices of Northeast Arctic cod (ages 0 and 1), and the biomass of mature capelin (see details in Stiansen *et al.*, 2005). According to Stiansen *et al.*, (2005), the presented models accounted for 65–85% of the variance in the predicted recruitment. For South African anchovy, "fluctuations in copepod biomass and production on the spawning grounds, the incidence of oocyte atresia in adult females, the incidence of southerly winds at Cape Point and the distance offshore of the 16°C isotherm at Cape Columbine were associated with fluctuations in anchovy recruitment" (Cochrane and Hutchings, 1995).

The dominant motivation for recruitment forecasting appears for management planning to ensure optimal harvesting strategies (see, e.g. Sun *et al.*, 2009). This is particularly true for cases where management advice is provided before the level of recruitment can be assessed and/or when management advice involves multi-annual decisions such as total allowable catch (TAC). An example is provided by the management of South African anchovy (*Engraulis encrasicolus*), where an initial TAC is set at the start of the fishing season in January, before the level of the year's recruits of 0-year-old fish can be quantified, and the TAC is readjusted in May or June after the actual recruitment has been estimated (Cochrane and Starfield, 1992). Simulation results show that for this particular stock, the average annual catch could be increased theoretically by up to 48% given very precise (CV = 0.1) short-term predictions of recruitment at the start of the fishing season.

Since management decisions are defined in terms of time horizons, forecasting SR has been classified as being *short*, *medium*, or *long term*. The classification, however, is non-unique, and has to be considered in relationship with the life cycle of the specific stock of interest. Northeast Arctic cod and Northeast Arctic haddock (*Melanogrammus aeglefinus*) stocks, for which recruitment to the fishery occurs at age-3, a short-term forecast is 1–3 years ahead, while for species like Greenland halibut (*Reinhardtius hippoglossoides*) and redfish (*Sebastes mentella*), short-term forecast may be as much as 6 years ahead (see ICES, 2011a). Both short- and medium-term projections are usually based on fitted stock–recruitment functions and recent trends in recruitment. The literature also reports recruitment forecasts based on historical estimates of recruitment, such as the projected short/medium-term recruitment being a geometric mean of past estimates of recruitment, or the geometric mean of past recruitment values that fall below the arithmetic mean of the historic stock–recruitment data (see, e.g. ICES, 2003). For South African anchovies, a short-term forecast is defined in terms of months (see Cochrane and Starfield, 1992). In general, however, short-term forecasts have been considered most reliable, which explains their popular use in stock assessment and in the context of management advice (see, e.g. Bogstad *et al.*, 2000). In contrast, the more uncertain medium- and long-term forecasts are more often used in the context of management strategy evaluations (MSEs; see, e.g. Kimoto *et al.*, 2007).

The literature reports mixed results when evaluating the practical implementation, effectiveness, and impact of forecasted fish recruitment on management decision. For California sardine, SST has been successfully used in predicting stock–recruitment (in the stock assessment) and therefore in the harvest control rules for this particular stock (Jacobson and MacCall, 1995; Deriso *et al.*, 1996). Conversely, using North Sea cod as an example, Planque *et al.* (2003) concluded that currently, there is limited managerial benefit of forecasting recruitment based on environmental information. This conclusion, however, does not discount the possible use of environmental information to forecast recruitment in the future. It merely emphasizes the fact that for this particular stock, there is limited understanding of the coupling between the environment and recruitment, which prevents reliable recruitment forecasts from environment-based recruitment models. The literature also reports of failure when harvest rules have been derived using environment-based recruitment forecasts. For instance in 1999, the TAC for the Bay of Biscay anchovy was drastically reduced when the projected SSB was found to be well below the precautionary SSB level. The projected SSB was based on predicted recruitment from a model that had previously shown a significant relationship between the upwelling index and recruitment of age-1 fish (see Borja *et al.*, 1998). On re-examination, the forecasted recruitment turned out to have been grossly underestimated. As a consequence, this particular environmental index is no longer considered a reliable indicator of the absolute levels of recruitment (De Oliveira and Butterworth, 2005). Based on simulation results, Cochrane and Hutchings (1995) report the possibility of obtaining a valuable increase in mean annual yield of South African anchovy fishery if below-average recruitment could be forecasted 6 months in advance of obtaining reliable measurements of recruitment, at the start of the fisheries.

Basson (1999) undertook a simulation study to investigate the value of including environmental data for management procedures, and arrived at the conclusion that there is no advantage in incorporating environmental drivers of recruitment in the short term for conservation or yields. Furthermore, there were situations where the incorporation of environmental factors made the management decisions worse. While these conclusions may appear to apply to some of the examples previously discussed (e.g. for the Bay of Biscay anchovy), the fact remains that each species (its life history and dynamics) and fishery needs to be carefully considered before being a candidate for the inclusion of environmental factors in recruitment forecasting.

Outstanding methodological challenges and caveats

Defining recruitment

One of the largest problems in contemporary discussions concerning SRRs is that the recruitment is neither to the fishery nor at the point of sexual maturity. While the point in the life history is not critical, the range of ages used mean that there is no consistency in the meaning of recruitment. In some instances, e.g. North Sea Autumn Spawning herring at age-0-winter rings, the year-class strength is apparent (ICES, 2013b), whereas in Northeast Arctic cod, processes such as cannibalism mean that the year-class strength may not be apparent until age-3 (ICES, 2013a).

Recruitment, in the strict fisheries definition (becoming vulnerable to the fishery or captured), is generally length or size dependent, rather than strictly age dependent. Likewise, recruitment to the adult, i.e. sexually mature, portion of the population is also primarily driven by length; however, age will also have an influence. Recruitment is assumed to be knife edged (in the case of sexual maturity, can be either deemed knife edged or, more commonly, may vary annually and is determined from surveys) and a convenient age class is chosen, often for simplicity, whereas it is well known that there is a selectivity curve for both capture and maturation.

To make matters more complicated, sometimes a year class that is not fully defined in regard to the life history, such as age 0, has been chosen in the past for age at recruitment to the fishery, e.g. Irish Sea cod (ICES, 2011b). To add to the confusion, spawning for some species occurs on either side of 1 January, i.e. 1 year class effectively spans two different years, e.g. north–east Atlantic herring (ICES, 2013b). In the case of North Sea autumn spawning herring, the 0-winterring (or 0-group) is clearly defined as 1 January, but the larvae are enumerated during a survey in February when they are nominally 3–4 months old (ICES, 2013b). This definition of year class is clearly not appropriate for many winter and spring spawning herring populations.

Modelling stock–recruitment

The existence of a spawners–recruits relationship (and its particular form) is often accepted without question in the fisheries literature. However, empirical evidence that such a relationship may occasionally fail to exist in general has been reported by Sakuramoto (2005) and, for Pacific Salmonids, by Peterman (1978). Myers and Barrowman (1995) undertook a meta-analysis of 364 spawner–recruitment time series and noted that, on average, the highest recruitment occurred at high spawner abundance and the lowest spawner abundance produced the lowest recruitment. These conclusions arising from the meta-analysis contradict, for instance, the (overcompensation) assumptions underlying the Ricker-type recruitment relationship.

Incorporation of environmental effects

A general potential challenge to methodologies for incorporating environmental factors into SRRs is the fact that such dependencies are usually non-linear and asymmetrical. Further, because the time series of data is usually short and noisy, estimation of the underlying coupling between recruitment and environmental parameters is difficult (see, e.g. Lungarella *et al.*, 2007). Attempts to accommodate co-incidental trends in time (Iles and Beverton, 1998) may also lead to development of models with little predictive ability (see Hilborn and Walters, 1992; Chen and Irvine, 2001).

The search for environmental influences on recruitment has resulted in many studies which incorporate physical factors into theSRR, e.g. NAO in North Sea autumn spawning herring (Gröger *et al.*, 2010), temperature with cod (O'Brien *et al.*, 2000), which was taken up in a wider study by Drinkwater (2005). Changes in recruitment have often been found to be indirect responses to changes in third factors (Drinkwater, 2005). For instance, temperature may cause shifts in the composition of the zooplankton community, and thus indirectly strengthen or weaken recruitment (Beaugrand *et al.*, 2003). Furthermore, factors such as upwelling, salinity, and sea level might correlate with temperature and have thus been hypothesized to be the actual causes of changes in recruitment (Prager and MacCall, 1993). Because the impact of temperature may often be an indirect response to changes in many other parameters, temperature has been be used as a proxy measurement of other environmental factors (see Jacobson and MacCall, 1995; Myers, 1998, and references therein). Temperature has also been shown to influence the spawning stock, the effects of which will eventually be seen in recruitment. For instance, Ottersen *et al.* (2006) investigated change in the relationship between sea temperature and recruitment of Atlantic cod over time and found that a decrease of length and age of average spawners occurred at the same time as a strengthening of the impact of temperature on recruitment. Direct temperature influence on spawning times and sites has also been reported by Morgan *et al.* (2013). Thus temperature may have indirect effects on recruitment, either through its links with the spawning stock or as a proxy for other (unmeasured) environmental variables.

In lieu of models of form (5)–(6) and (8), a model that incorporates the effect of temperature could, in general, have the form described by Equations (12)–(13):

$$R = f\,(S(E)), \tag{12}$$

$$E_t = g(A^{(1)}_{t-\tau_1}, A^{(2)}_{t-\tau_2}, \ldots, A^{(n)}_{t-\tau_n}), \tag{13}$$

where there is a causal link between S_t and a finite n number of environmental factors, $A^{(j)} \leq ft(j = 1, \ldots, n)$, through E_t. The causal link is indicated by the time-lag, $t - \eta_j$, between E_t and each environmental factor. Thus formulated, the function E_t could be a linear or non-linear function of environmental factors or even proxies (e.g. temperature).

Fitting stock–recruitment functions

It is worth noting that most of the literature on classical models and assumptions of recruitment are dominated by empirical data and analyses of Salmonid stocks (see, e.g. Allen, 1973; Peterman, 1978, 1981). For such stocks (in particular, the sockeye salmon *Oncorhynchus nerka* population in the Skeena River), Walters and Hilborn (1976) cite Allen (1973) in arguing that empirical evidence in support of the lognormal distribution exists, while Hilborn (1985) cites Peterman (1981) for the same reason. It is also worth pointing out that the distribution of recruitment can vary for many reasons, including the influence of stock size or structure (Hsieh *et al.*, 2006; Anderson *et al.*, 2008) or due to productivity regimes (Vert-pre *et al.*, 2013). It is conceivable, however, that this assumption may fail to hold, for instance, for stocks with stable stock sizes, which are less prone to extreme fluctuations. In the statistical description of recruitment for 18 stocks, Hennemuth *et al.* (1980) report that Georges Bank cod and Peruvian anchovy (*Engraulis ringens*) exhibit normal rather than lognormal distributions, while multimodal distributions appeared to be more descriptive of both Georges Bank haddock and Northeast Arctic haddock. According to Hennemuth *et al.* (1980), "most well-known standard, single or even joint probability distribution functions do not account for the frequency of occurrence in the long right-hand tails observed in some cases". If it cannot be established, the assumption of a lognormal distribution may lead to biased parameter estimates, although it affords computational ease (see, e.g. Walters and Hilborn, 1976).

The issue has additional complexity associated with how the error structure in the dependent (recruitment) variable relates to that in the independent variable (spawning stock). Although not explicitly stated in most cases, the assumption in the literature is that the error term on the right-hand side of the recruitment function captures the uncertainty in the dependent variable, which also includes the stochasticity observed in the independent variable. It is not unusual, however, that both the recruitment and SSB are characterized by different variances and error distributions. It is not uncommon that the SR data are characterized by a general lack of contrast in the independent variable (usually SSB) coupled with highly variable recruitment. Then given the assumption that the two variables are independent and normally distributed, the solution obtained will very much depend on the ratio of their variances.

In the fisheries literature, the issue of separate error structures in the recruitment and spawner data failed to receive further attention after it was first discussed in Ludwig and Walters (1981b). If ($\hat{R}_t$, $\hat{S}_t$) represent observations of the true recruitment and SSB values (R_t, S_t), then separable error structures imply that

$$\hat{R}_t = R_t + \varepsilon_t, \tag{14}$$

$$\hat{S}_t = S_t + \eta_t, \tag{15}$$

where ε_t and η_t can, for instance, be assumed to be independent and normally distributed. It must be recognized that this is a potential source of bias when deriving SR functions and that standard linear regression methods in such cases will yield suboptimal solutions (Cornbleet and Gochman, 1979); see also discussion in Ludwig and Walters (1981b). The problem is best solved using an errors-in-variables model or methodology, which seeks to account for errors in observations on both the independent ($\hat{S}_t$) and the dependent ($\hat{R}_t$) variables. An example methodology is the Deming regression approach (Martin, 2000). The methodology is equivalent to a maximum likelihood estimation procedure in which the errors for the two variables are assumed to be independent and normally distributed, while the ratio of their variances, $\delta_t = (\varepsilon_t/\eta_t)$, is known (e.g. estimated from data) (Linnet, 1993).

Of all the possible sources of uncertainty, structural uncertainty remains one of the most challenging issues in fisheries science (Hammond and O'Brien, 2001) and, in particular, to the task of fitting stock–recruitment functions to observation data. The choice of recruitment function (e.g. Ricker, Beverton–Holt) may be wrong (Patterson *et al.*, 2001), or there may be aspects of the dynamics that the rigid analytical functions are incapable of capturing (Mace and Sissenwine, 2002). This is understandable given the absence of data and rigorous statistical techniques to explore the basic assumptions of the nature of density dependence and other biological processes that underpin the SRRs. Thus, the choice of recruitment model remains a major source of uncertainty in the fitting process.

For almost identical goodness-of-fit values, Myers *et al.* (1994) obtained different functional results for the Ricker and Beverton–Holt models (Barrowman and Myers, 2000; Williams and Shertzer, 2003). With respect to analytical stock–recruitment functions, a more central and basic issue is the fact that models with a small number of parameters are fit to data. Regardless of whether the Deriso, Beverton–Holt, or Ricker models are used, the fact remains that these analytical functions do not possess enough flexibility in their definitions to allow any deviations from the presumed recruitment–spawning stock relationship, even if the data dictate otherwise. Though the diagnostics of the fitted stock–recruit model should indicate that the fitted model is incorrect, this conclusion may not be exclusively valid (see, e.g. de Valpine and Hastings, 2002), given the nature of the data.

In the literature, the Akaike information criterion (AIC) and Bayesian information criterion (BIC) (see Burnham and Anderson, 2002) have been employed in the selection of SRRs (see, e.g. Wang and Liu, 2006; Shimoyama *et al.*, 2007). Indications from the literature are that the use of AIC or BIC as selection criteria can be potentially misleading. While Wang and Liu (2006) compared and found both the AIC and BIC as valid selection criteria, simulation studies by de Valpine and Hastings (2002) indicate that the Ricker model gave a better fit to the data than the Beverton–Holt model, when the AIC was used to select the best-fit model. Furthermore, though the Beverton–Holt model generated the data, the AIC selected the Ricker model as best fit. For typical fishery data, Zhou (2007) reports the probability of selecting the correct model based on information criteria to be 0.70 and 0.61, respectively, for the Ricker and Beverton–Holt models. In general, the task of choosing the *best* model among a variety of candidates is a statistically challenging and non-trivial problem. For a review, see de Gooijer *et al.* (1985). When short time-series are used as input, it is hard to distinguish between closely related models (based, e.g. on AIC, BIC) since selection indices tend to be very close to each other. A change in, for instance, the length of the input data may result in a different model choice, and consequently in the forecast. See a detailed discussion in Zou and Yang (2004).

A completely different approach to the use of rigid analytical functions will be to posit (either the Beverton–Holt or Ricker type) dynamics behind the SRR relationship, based on some *a priori* knowledge (e.g. ecological/biological), then allows the data to "speak for itself". To illustrate, suppose we introduce a parameter transformation $u = R/S$(for $S > 0$) into the Beverton–Holt and Ricker functions (this also holds for the Deriso function for which the Ricker and Beverton–Holt models are special cases), we obtain

$$u(S) = \begin{cases} \mathrm{e}^{\alpha-\beta S}, & \text{Ricker}, \\ \dfrac{\alpha}{1+\beta S}, & \text{Beverton-Holt}. \end{cases} \tag{16}$$

We can then prove (maintaining the original constraints on α and β) that u is both monotone and convex. An immediate consequence of this transformation is that one can write

$$u(S) = \sum_{i=1}^{N} c_j B_j(S),$$

where $B_j(S)$ represents a set of basis functions with some local support (e.g. low degree splines) and c_j are a set of parameters to be determined. It is then possible to solve for u by imposing constraints on c_j such that the derived solution has the required properties. Once u is obtained, R can be recovered. Bravington *et al.* (2000) and later, Cadigan (2013) who fitted a non-parametric stock–recruitment model using the R-SCAM package (Pya, 2010, 2013), are based on such an approach. This approach (reparametrization using B-spline basis functions) has the attraction that the spline knots (design points) can be chosen independent of the observation. There are two potential challenges. The choice of an arbitrary high number N of basis functions may result in oscillatory (non-monotonic), and biologically implausible solutions. In the R-SCAM package, regularization of the problem is addressed by adding a term in the objective function with a smoothing parameter, which penalizes divergence from smoothness. The actual choice of the smoothing parameter, which can be determined by, for example, generalized cross-validation (GCV), is usually data dependent (see, e.g. Wahba, 1985). More generally, the choice of penalizing term and how it is determined will dictate the type of solution obtained. For instance, methods such as GCV and unbiased risk have been developed under the assumption that the data are from independent observations (Wang, 1998). When the independent observation assumption is violated, the results obtained are underestimates of the optimal smoothing parameter. If this approach (reparametrization using basis functions) is to be truly generic, the following must be considered (i) since the fitting problem involves more than data interpolation and smoothing, it must admit other basis functions which possess the same flexibility and continuity properties as B-spline, e.g. Hermite or Bernstein polynomial (see, e.g. El Attar, 2006); (ii) rather than being explicitly imposed on the solution, the degree of smoothness of the SR function must be an emergent property of the derived function; and (iii) given the nature of the SR data, the parameter estimation must be robust to outliers and computationally feasible, even for a very small number of observation. Following the discussion from the previous paragraph, non-parametric recruitment models of the type described in this paragraph (despite their attractiveness) must still be regarded as candidates in an ensemble of several possible explanatory models (both parametric and non-parametric).

Forecasting stock – recruitment

The problem of forecasting stock–recruitment shares several common characteristics with that of finding a functional fit to, for example, recruit-spawner data. The shared characteristics include (but are not limited to) decision on model choice (type and degree of complexity), issues with bias-variance trade-off, and effect of underlying statistical assumptions on estimated model parameters. However, recruitment forecasting presents an additional challenge since it seeks to address the problem of making statements about the most likely outcome of future values of a process (or time-series variable) whose actual outcomes are unknown. The outstanding problems with recruitment forecasting are therefore many, and deal with issues concerning the process, accuracy, and relevance of forecasts.

Why has the SST-based forecast of California sardine recruitment (Jacobson and Mac-Call, 1995) been successful, while the potential of a similar SST-based recruitment forecasting of, for example, North Sea cod (Planque *et al.*, 2003), been considered ill-advised? This is because the assumed SST–recruitment relationship for the California sardine turned out to be a (non-linearly) causal relationship (Sugihara *et al.*, 2012). Since recruitment is forced by several drivers (including temperature), it is conceivable that not all factors will have direct (linear/non-linear) causal link to recruitment, and that one or several links may be transitive. The correlation between SST and recruitment may be high (even in the absence of a direct causal link) when temperature represents the most viable proxy for the group of recruitment driving forces or the common denominator for a series of transitive relationships. On the other hand, correlations between covariates could be weak although a causal relationship exists. For instance, the observed correlations in the relationship between the 3-year running averages of the Scripps Pier SST–sardine recruitment and spawning stock size by Jacobson and MacCall (1995) appeared to vanish, when the analysis was extended to include assessment results from 1992 to 2009 (see McClatchie *et al.*, 2010; Sugihara *et al.*, 2012). Another good illustration is provided by an example model by Stiansen *et al.* (2005), which provides a two year-ahead forecasts for 3-year-old recruits of Northeast Arctic cod,

$$R_t \sim (\text{Water Temp.})_{t-3} + (\text{Age} - 1\ \text{cod})_{t-2} + \log(\text{Biomass of Matured Capelin})_{t-2}. \qquad (17)$$

Retrospective analysis (from 1984 to 2004) showed that the model could explain ∼85% of the recruitment variation. A recent (2012–2014) re-examinations show that the model forecasts for the past 5 years account for <50% of the annual recruitment variability (see ICES, 2012). The model's poor performance can be linked to the inability of the environmental indices (age-1 cod, biomass of matured capelin, and perhaps water temperature) to capture components of the state-dependent dynamics of the ecosystem that appears to force the stock–recruitment.

In practice, one is often faced with an array of environmental indices (or indicators) as candidates covariates for the forecast model. Two outstanding challenges in developing recruitment forecast models then emerge. First, relevant causal indices must be identified among candidate environmental covariates using robust methodologies other than correlations. For fisheries data, this challenge has an additional component because detecting causalities may call for longer time series than is usually available. Second, models must be formulated such that the environmental variables are state-dependent rather than fixed indices (see Sugihara *et al.*, 2012). This second consideration alludes to the development of models that incorporate environmental indices in a state-space framework. The state-space framework is particularly attractive for recruitment forecasting because it separates parameter (and observation) uncertainty from demographic variability. The variance of unexplained demographic variation is necessary to accurately represent the total stock–recruitment uncertainty. In general, parametric uncertainty can be reduced by improving the information content (or accuracy) of the data used in estimating model parameters. Unfortunately, uncertainty in projections due to demographic uncertainty generally cannot be reduced, particularly in medium and long-term projections.

The existence of multiple environmental indicators of recruitment, however, implies the possible development of several candidate forecast models on subsets of the pool of data. For example, about eight different regression models currently exist for forecasting age-3 recruits of Northeast Arctic cod. The models take as input different combinations of data from a time-series pool consisting of oxygen saturation at bottom layers of the Kola section transect (stations 3–7), the air temperature at the Murmansk (Russia) station, water temperature (stations 3–7) of the Kola section (layers 0–200 m), ice coverage in the Barents Sea, abundance indices from acoustic and bottom-trawl surveys, and biomass of fish. In the absence of an absolute truth for future estimates of recruitment, each of the model forecasts constitutes a plausible truth. Further, when candidate models use different datasets or different combinations of such in the modelling process, choosing a *best* candidate model becomes an even more challenging task especially when the variable to be forecasted is inherently highly uncertain. Combining individual model forecasts as introduced by Bates and Granger (1969) is often considered as a successful alternative to using just an individual best model. Furthermore, there is theoretically proven advantage of a proper combining over any selection method (see Yang, 2004). Specifically for time-series forecasting, predictive performance increases (Makridakis and Winkler, 1983; Armstrong, 1989; Clemen, 1989). A viable alternative to model selection has been to admit a plurality of candidate models (Ricker, Beverton–Holt, etc.). In Jiao *et al.* (2009), a representative value for recruitment was found by Bayesian Model Averaging (Hoeting *et al.*, 1999) applied to an ensemble of model solutions. It must be kept in mind that the variance across a number of models is related to the risk of selecting among these models (see Vapnik, 2000; Bousquet and Elisseeff, 2002). Hence, for any measure of variance, the goal of combining individual forecasts will be to reduce the variance of the performance across the combinations relative to the variance across the individual methods (Breiman, 1996; Evgeniou *et al.*, 2004).

Even if the computational challenges and complexities involved in developing good recruitment forecast models are addressed, the fact remains that the models forecasts are inherently uncertain. This begs the ultimate question: "what is an acceptable degree of uncertainty in a recruitment forecast?" Perhaps the answer lies in the goal of the recruitment forecast. From a managerial point of view, this question translates into how accurate environmental-dependent forecast models have to be to be considered as management decision tools (De Oliveira and Butterworth, 2005). In this context, an acceptable degree of uncertainty translates into a tolerable management decision risk in setting TACs and other harvest rules. In a controlled numerical experiment, De Oliveira and Butterworth (2005) concluded that an environmental index need to explain at least 50% of the total variation in recruitment before the management procedure starts showing benefits, measured in terms of the summary statistics for risk and average catch. There is, however, room for further research in this area, when model forecasts are based on short-time-series data. In particular, there is a requirement for methodologies for predicting, quantifying uncertainty and risk associated with rare events (recruitment spikes).

Concluding remarks

As stated by Hilborn and Walters (1992), "Analysis of stock–recruitment data provides an enormous number of traps for the unwary—good luck". This statement becomes even more poignant when attempting to include the effects of environmental variables in recruitment modelling and prediction. While theoretical reasons (Bradford, 1992; Mertz and Myers, 1995) establish doubt over whether recruitment will ever be predicted with the degree of accuracy needed for management purposes, incremental progress has been made in the past 100 years; techniques are now available (e.g. linked biophysical IBMs, conceptual modelling, more robust analysis of empirical information) that provide a firm groundwork for further investigations. For instance, within the domain of coupled biophysical IBMs, three broad categories of hypotheses have been identified to explain and predict recruitment variability in fish populations (Miller, 2007). Studies show that recruitment variability may be related to food and growth, transport, or predation, and most of the hypotheses (see, e.g. Cowan and Shaw, 2002; Govoni, 2005) clearly point to coupling between physical and biological processes as key to understanding recruitment variability. Ecological concepts continue to be translated with success into methodologies and models, which when pooled together, are capable of explaining and interpreting different aspects of recruitment variability (see, e.g. Minto, 2011). Several statistical tools have evolved (e.g. randomization tests) that provide robust analysis of empirical information. Such tests can be used to check the statistical characteristics of data, such as independence of observations, or to screen goodness-of-fit tests (Stephens, 1974). Power (1996), for instance, applied randomization and goodness-of-fit tests to recruitment dataseries for several hundreds of North Atlantic fish stocks to establish the suitability of the exponential, lognormal, and Weibull distributions as representing appropriate descriptions of the data.

The central question remains: "will stock–recruitment modelling and forecasting be recognized as being relevant to fisheries science and management in the next one hundred years?" While believing this is possible, there are prerequisites for success. The purpose of recruitment models needs to be identified and clarified before development, i.e. the models must be developed and tuned to specific goals and objectives. This calls for two distinct lines of recruitment modelling, dictated by whether the goal is to address policy-relevant issues or to understand cause–effect mechanisms. Management decision models for instance, must be required to satisfy some decision calculus, i.e. a set of numerical procedures for data processing and judgement, to qualify as decision tools. These model requirements include (see, e.g. Little, 2004) (i) completeness and parsimony—incorporating only the most important drivers influencing decision parameters; (ii) robustness—providing plausible, non-absurd results; (iii) controllability—knowledge of type of input data required to produce a desired output; (iv) adaptiveness—seamless incorporation and accommodation of new information with the goal to improve model performance; and (v) possession of a simple interface for evaluation of risk and decision effects, e.g. of how a change in model parameters may impact management decision. While parsimony remains a guiding modelling principle, models built purposely to understand recruitment mechanisms may need to be adequately complex, i.e. incorporate community dynamics and environmental factors, to fully integrate recruitment drivers. Such process models must also be able to produce a larger spectrum of results other than observations, which only constitute a snapshot of natural variability. Thus all model scenarios that do not violate first biological/physical principles may be considered as plausible (contrast with (ii)–(iii) for management decision models). Finally, for process models, risk and decision effects are secondary to the primary quest to understand the different configurations of driver alignments and how these may result in different observation states. In the recognition and pursuance of this dichotomy lies the path to relevance and success for stock–recruitment modelling and forecasting.

Do we need the whole life cycle for assessment purposes? The answer may be "probably not" for applied purposes. Keeping the analyses as simple as possible while understanding the limitations may be good enough to assessment and management. Recruitment models for such purposes (e.g. determining reference points or MSE) could be formulated, for instance, in terms of management parameters (e.g. maximum sustainable catch and harvest rate) rather than productivity parameters, making them more relevant to policy (see, e.g. Schnute and Kronlund, 1996). On a cautionary note, the user should be extremely aware of how the recruitment data were generated (see Dickey-Collas *et al.*, 2014). Often recruitment time series are outputs from standard stock assessments and are therefore the consequence of the assumptions in the assessment model. Further, since the outputs from different models give different perceptions, quantifying uncertainty in model predictions must be an integral component of the modelling exercise. Shorter time series are available from survey indices, which, while they are free from the assumptions in the assessment model, are influenced by assumptions in survey design and strategy.

Apart from providing support to policy decisions, recruitment modelling could be the result of a quest to understand cause–effect mechanisms underpinning stock variability, and this may require considering life histories and the drivers of early life-history dynamics, including parental effects, as well as endogenous and exogenous influences on survivorship through to sexual maturity. For this purpose, a life-stage model may be essential; here, success is required in further development of predictive modelling tools to fully link recruitment variability to perturbations in biotic and abiotic conditions. This idea is in itself not new (see, e.g. Myers and Drinkwater, 1989; Myers, 1998), however, in this particular context, the term "predictive modelling" is used in a broader sense to describe two major tasks, namely (i) the ability to develop models based on established causal links in the mechanisms (biotic and abiotic, across populations, and on different time and data resolutions) during different life stanzas of fish growth and (ii) to demonstrate that these mechanisms determine the dynamics of recruitment, based on more robust methodologies other than correlations (Myers, 1998). Many have even gone as far as questioning the utility of funding research in recruitment, which incorporates environmental indices (see Myers, 1998; Walters and Collie, 1988). The crux of the problem, however, lies in the statement by Myers (1998): "The emphasis on the search for environmental *correlations* of recruitment may have led to the neglect of other important processes" (emphasis on correlations by us). Further, although recruitment forcing may be better understood when studied across populations (Myers and Barrowman, 1995; Myers, 1998), the basic challenge remains: the information available for most exploited stocks is inadequate for precise modelling, even for those species which have long-time series (e.g. North Sea or Barents Sea gadoid stocks). It will therefore be essential to harness efforts being made in various fronts, including linked biophysical IBMs, conceptual modelling, and field experiments to understand mechanisms regulating interannual survival at the egg and larval stages.

There is no doubt that, in an ever changing climate, recruitment modelling and forecasting will remain central to fisheries science in the next 100 years. Recruitment models will be required to develop and evaluate harvest control rules in management plans, set precautionary and MSY reference points, and predict likely changes to stock productivity caused by changes to habitat, regime, or local climate. While the task involved is far from simple, developments in recent years (in field experiments and conceptual modelling) give grounds for optimism.

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Handling editor: Mark Maunder

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2323–2342. doi:10.1093/icesjms/fsu048

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Original Article

A risk-based approach to evaluating northeast US fish community vulnerability to climate change

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Gaichas, S. K., Link, J. S., and Hare, J. A. A risk-based approach to evaluating northeast US fish community vulnerability to climate change. – ICES Journal of Marine Science, 71: 2323–2342.

Received 1 July 2013; revised 14 February 2014; accepted 25 February 2014; advance access publication 8 April 2014.

Risk assessment methods are used worldwide to evaluate threats posed by fisheries and other impacts on living marine resources, and to prioritize management of these threats. We derive a simplified risk analysis for aggregate fish communities as a preliminary tool to identify priorities for further detailed assessment. Because some of the largest observed rates of sea surface temperature increase are on the northeast US continental shelf, we focused on climate change-driven risks to marine communities in this region. We evaluated climate vulnerability for six communities across two ecosystems: both commercial and non-commercial demersal fish, pelagic fish, and benthic invertebrates in the Gulf of Maine (GOM) and Mid-Atlantic bight (MAB). We first evaluated the probability that anticipated climate changes (e.g. warming water, decreased salinity, increased acidity, altered boundary currents) would occur in these regions, and rated the potential severity of change over the next 10 years. Then, we evaluated the sensitivity of each biological community in each region using 12 attributes (e.g. habitat and prey specificity, temperature and acidity sensitivity, larval dispersal, adult mobility, population productivity, etc.). Exposure to the key climate risks was related to community sensitivity in each region for an overall assessment of climate vulnerability. Climate risks from increased surface water temperature, sea level rise, and earlier spring were rated moderate to high in both regions, with additional moderate to high risks in the GOM from increased bottom temperature, stratification, and river inputs. Benthic invertebrates were rated most sensitive, with demersals intermediate and pelagics lowest. Two MAB communities were rated more sensitive than corresponding GOM communities, but greater short-term climate risks in the GOM indicated increased exposure for GOM communities. Overall, this simple analysis may help prioritize short-term regional climate risk management action, thus addressing key conditions related to fishery fluctuations beyond fishing itself.

Keywords: benthic invertebrates, climate vulnerability, commercial fisheries, demersal fish, ecological risk assessment, non-target species, northeast US, pelagic fish.

Introduction

> In order to understand the fluctuations of the fishery, it is therefore evidently highly necessary to be acquainted with the variations of the year classes; it must, however, continually be borne in mind that other conditions may also play an important part. (Hjort, 1914, p. 43)

Quantitative single species stock assessment is currently the major tool to estimate the fluctuations of fisheries and consider these fluctuations in management advice throughout the world. In the 100 years since Hjort's groundbreaking work, characterizing variation in year-class strength (recruitment) has become an important focus of fisheries science and stock assessment (e.g. Kendall and Duker, 1998), along with estimating fishing mortality (Schaefer, 1956; Smith, 1994) However, it is also increasingly apparent that the "other conditions" contributing to fishery fluctuations require attention as well, as suggested by Hjort and Schaefer (Schaefer, 1956; e.g. pollution, habitat alteration, species interactions, and environmental variability). A contemporary of Hjort, Spencer Baird, noted as much when he called for an inclusive research programme to explore the changes in fish year class variability in New England, particularly invoking the need for studies on "peculiar atmospheric agencies, such as heat..." (Baird, 1873). While it is possible to include other conditions in stock assessments (Keyl and Wolff, 2008; Link, 2010; Wayte, 2013), it is often difficult and costly to do so, and many factors may alter fish population trajectories (*sensu* Gaichas *et al.*, 2012; Link *et al.*, 2012). Many stock assessments estimate statistical error in recruitment, thus potentially accounting for the subset of Hjort's other conditions that explain recruitment variability. However, if other conditions drive trends (rather than variation) in recruitment, change productivity regimes, or pose a substantial threat to the stock that is not currently accounted for in the assessment, there is a risk of getting stock assessments and associated management advice wrong. Given the large number of fished stocks and other conditions, some form of "triage" evaluating this risk among stocks is warranted (Link, 2002).

Ecological risk assessment is a promising tool for systematically and transparently addressing and prioritizing Hjort's "other conditions" which may pose threats to fishery stocks. Generally speaking, risk assessment is a process to evaluate the potential, magnitude, and consequence of negative events occurring. This is a best practice adopted originally from business management fields and encoded by the International Standards Organization (ISO) standard 31000 (ISO, 2009a, b, c). The ISO standard bases risk management on a three-step risk assessment process: identification, analysis, and evaluation, which ultimately determines whether risk treatment is required to meet management objectives. Built into the standard are requirements for risk communication, consultation, review, and continued monitoring. The advantage of this approach is that it is consistent, transparent, and standardized. Furthermore, the approach has been adapted to evaluate a wide range of environmental issues (e.g. US EPA, 1998; Standards Australia, 2012; Cormier *et al.*, 2013) including some instances of risk assessment for fisheries stocks (e.g. Fletcher, 2005; Smith *et al.*, 2007; Martin-Smith, 2009; Patrick *et al.*, 2010; Hobday *et al.*, 2011; Hollowed *et al.*, 2013). Despite some contrasts in the application of risk assessment frameworks, and regardless of application to environmental management, fishery management, business management, etc., the risk assessment process remains similar. There are commonalities across all frameworks, including an initial triage or scoping phase to identify priority risks to achieving management objectives, the use of clearly defined qualitative or quantitative criteria to analyse priority risks over a variety of attributes, and the evaluation of scientific certainty or reliability of information within assessments. Risk analysis is also a specific component of the Levin *et al.* (2009) Integrated Ecosystem Assessment (IEA) framework, so these methods are applicable both in a fisheries assessment context and in an ecosystem assessment context (e.g. Samhouri and Levin, 2012; Chen *et al.*, 2013). Here we use them as a bridge between the contexts, as an example of risk assessment's utility to prioritize among Hjort's "other conditions", and an initial step towards identifying and including key ecological interactions in the assessment and management of fisheries in the Northwest Atlantic.

The Northeast US continental shelf (NE shelf) has experienced the largest change in thermal conditions observed in temperate waters off North America (Rayner *et al.*, 2003; Wu *et al.*, 2012; Hobday and Pecl, 2013). The oceanographic environment has experienced notable shifts, including warming, freshening, increased stratification, and changes in circulation (EcoAP, 2012; Smith *et al.*, 2012). Climate-related change in the ocean has impacted fish stocks in this region including productivity (Fogarty *et al.*, 2008), recruitment (Hare *et al.*, 2010), distribution (Rose, 2005; Nye *et al.*, 2009, 2011), mortality (Weinberg, 2005), and fishing patterns (Pinsky and Fogarty, 2012). These climate-related changes impacting fish stocks are in addition to fully utilized fisheries that have experienced sustained high fishing pressure (Boreman *et al.*, 1997; Link *et al.*, 2011). To achieve sustainable fisheries catch and population rebuilding objectives, Hjort's other conditions may need to be accounted for in the region's fisheries assessment and management. A risk assessment of the fish communities in this region relative to climate change effects could serve as a means to highlight those stocks most vulnerable to these other conditions. Certainly more detailed analytical tools, more species-specific examinations, and more detailed vulnerability assessments are needed in this and other ecosystems, but an initial risk assessment to "triage" across major fish communities also has merit to scope out where such future efforts should focus (e.g. Pecl *et al.*, 2011; DFO, 2012; Doubleday *et al.*, 2013).

Here we aim to first evaluate the potential risk of climate-related changes in the short term (up to 10 years in the future), with assessment of both probability and certainty of impacts in an extremely simple preliminary analysis. We then develop a simple application of risk assessment methods to specific biological communities compared across two ecosystems to ascertain both the sensitivity and exposure to climate effects in the near-term future. We do so to illustrate how this approach can permit scientists and managers to focus limited resources on assessing and/or managing for the "other conditions" most likely to influence fishery fluctuations.

Methods

To illustrate how risk assessment can contribute to understanding the "other conditions" leading to stock fluctuations, we apply a simplified hierarchical risk analysis framework (Hobday *et al.*, 2011) to northeast US fish and invertebrate communities as a preliminary tool to identify priorities for more detailed assessment and potential risk management. Hobday *et al.*'s (2011) framework begins with scoping to clarify assessment units, boundaries, and objectives, then proceeds through a series of analyses (Levels 1, 2, and 3) that increase in detail and specificity as they focus on fewer, higher risk situations. Our steps include scoping and identifying the relevant units for assessment, then conducting qualitative Level 1 risk analysis, followed by semi-quantitative (employing ranked scores, rather than full mathematical models (Sumner *et al.*, 2004)) Level 2 analysis. Level 3 risk analysis involving detailed quantitative models is beyond our scope here, although our work identifies priorities for such analyses. An overview of our workflow is given in Box 1, and details are provided in the sections below.

Scoping

Common features of all risk assessment frameworks include clear statements of scope and objectives as initial steps (e.g. Fletcher, 2005). While many possible hazards face marine ecosystems, we limit our scope to risk assessment of climate impacts to fish and invertebrate communities of the NE shelf region because some of the largest rates of sea surface temperature increase observed worldwide are in the Northwest Atlantic (Rayner *et al.*, 2003; Hobday and Pecl, 2013), and because fishery fluctuations are pronounced and of continuing interest in this region (Friedland *et al.*, 2008, 2013; Richardson *et al.*, 2011). Although climate projections are often for 50–100 years in the future, resource managers are generally concerned with shorter time horizons. Therefore, we limit the temporal scope of our risk analysis on the immediate fisheries management time horizon of 5–10 years, and base our analysis of climate impacts on the recent 5 years relative to a historical baseline (1960–1990). Within this temporal scope, we include components of both natural climate variability and long-term climate change.

Box 1. Steps in this risk analysis.

Scoping
Overall objective: Identify and prioritize risks
Audience: Regional fisheries science and management
Which risks? Climate related changes
Timescale: Fishery management horizon; 5 – 10 years from the present

Level 1
Objective: Quickly identify important climate impacts on biology, and information gaps
Risk to? Generalized marine fishery resource (fish or invertebrate)
Spatial scale: Northeast US continental shelf
Analysis:

1. Identify anticipated climate-related changes in the region
2. Identify biological processes of interest to fishery management
3. Qualitative assessment of whether each climate-related change would impact each biological process, with confidence rating

Level 2
Objective: Assess and rank specific climate risks to specific resources in two ecosystems
Risk to? 6 fish and invertebrate groups:

Commercial pelagic fish	Non-target pelagic fish
Commercial demersal fish	Non-target demersal fish
Commercial benthic invertebrates	Non-target benthic invertebrates

Spatial scale: 2 ecosystems: Mid Atlantic Bight (MAB), Gulf of Maine (GOM)
Analysis:

1. Assess climate risks for each ecosystem

1. Assemble climate indicator time series in each ecosystem, refined from Level 1 part 1.
2. Qualitative probability of occurrence for each anticipated climate related change
3. Quantitative assessment of severity from climate indicator time series in each ecosystem
    1. Degree of recent 5 years difference relative to baseline years
    2. Duration of recent change
    3. Trend of recent change
    4. Spatial scale of recent change
4. Assess overall climate risk by ecosystem, combining probability and severity rankings

2. Assess community sensitivity by ecosystem

1. Identify representative species for each community in each ecosystem
2. Qualitative assessment of biological sensitivity for each community in each ecosystem
    1. Life history traits rank community sensitivity low-high for 12 attributes
    2. Attributes equally weighted in overall summary sensitivity score

3. Assess overall community vulnerability to climate risks by combining 1 and 2

1. Qualitative assessment of community exposure to climate risks and sensitivity
    1. Community (habitat)-specific weighting for importance of each climate attribute
    2. Ecosystem-specific climate risks for each attribute combined with community specific weighting to get community exposure by ecosystem
2. Assess overall vulnerability by ecosystem, combining climate exposure and community sensitivity rankings

We have selected short-term and regional ecosystem spatial scales for risk analysis to simplify this example, recognizing that climate risks may change when viewed at longer time scales and either smaller (local) or broader (entire shelf or basin) spatial scales; the methods we demonstrate here could be used at any scale where information is available for analysis.

Scoping has clarified our overall objective: to assess the risk posed by climate-related changes (including both climate change and climate variability) on Northeast US marine communities, specifically to inform fisheries management. To achieve this, we performed a Level 1 risk analysis to quickly outline which biological processes for generalized marine resources are most susceptible to which climate impacts, and a Level 2 analysis to assess risks to specific communities by evaluating their particular vulnerability to the most important climate change impacts observed or expected in each ecosystem. Assessment units and spatial scale also increase in specificity from Level 1 to Level 2. At Level 1, we analyse climate risks to a generalized marine organism on the NE shelf. At Level 2, we evaluate potential impacts on six communities (both commercial and non-commercial groups in three habitats: demersal fish, pelagic fish, and benthic invertebrates) and we compare across these communities for two ecosystems (with boundaries as defined in the Northeast Fisheries Science Center's Ecosystem Status Report (EcoAP, 2012)): the Gulf of Maine (GOM) and Mid-Atlantic bight (MAB; Figure 1).

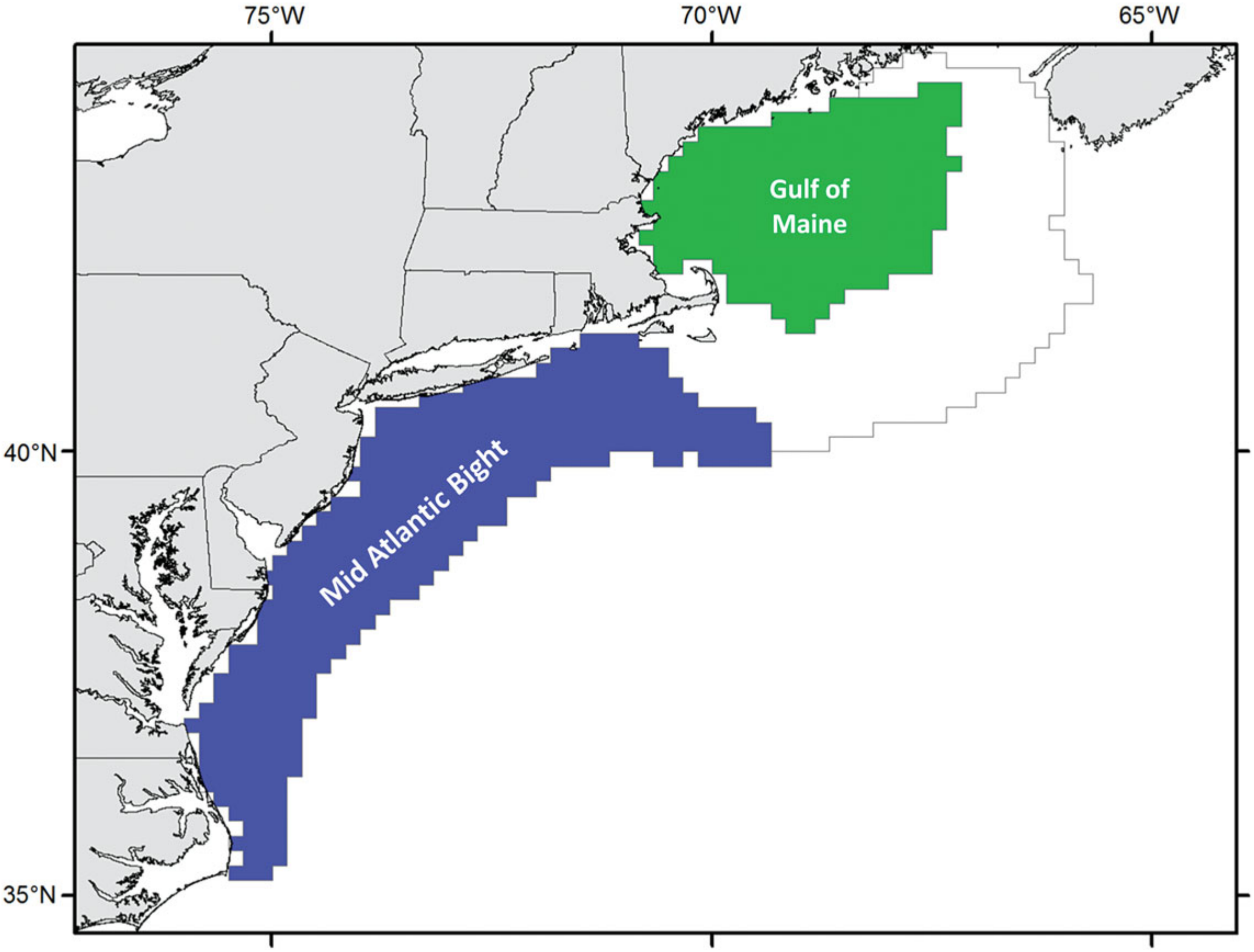

Figure 1. Map of the Northeast Shelf, which includes the Mid-Atlantic Bight and Gulf of Maine ecosystems. The full extent of the Northeast Shelf region also includes the area outlined in grey.

Level 1 analysis

In this initial analysis, we used expert opinion (of the authors) to quickly determine which climate impacts might be most likely to impact a general fishery organism on the Northeast shelf. The primary purpose was to identify high-priority climate/biological interactions of interest to fishery management, as well as where further information may be needed. We first outlined specific anticipated effects of climate-related change. We began with a list of anticipated climate changes identified for Northwest Atlantic basin (Harris and Tyrrell, 2001; Scavia *et al.*, 2002; NCIA, 2006; Frumhoff *et al.*, 2007; Drinkwater *et al.*, 2009; Doney *et al.*, 2012): warmer water, changing volume of thermal habitat, shifting local hydrography (e.g. fronts, local winds and currents), changing large-scale hydrography (e.g. altered boundary currents), changing water chemistry (fresher, more acidic, lower oxygen), changing primary production and other bottom up forcing, and changes in species composition including invasives, or natives from other regions. Similarly, we outlined the potential biological responses to these climate pressures. At the community or population scale, the basic biological attributes regulating population fluctuations (and therefore of interest to fishery management) include productivity, physiology, process timing or phenology, ecological context (primarily predator–prey and competitive interactions with other species), and spatial distribution (both range and centre) (Rose, 2005; Fogarty *et al.*, 2008; Nye *et al.*, 2009; Rijnsdorp *et al.*, 2009; Hare *et al.*, 2010).

We then examined each pair of climate attributes and biological responses and asked first whether we expected a change in that biological response as a result of that climate attribute (Y—yes, N—no, or M—maybe), and if a response was predicted, whether we could predict a general direction of change. We expressed our confidence in these ratings on a scale of 1–5, with 1 being low confidence and 5 being high. We conducted this analysis as a group among the authors and reached group consensus about our ratings. Our rationale for assigning ratings was as follows: ratings of Y (yes) or N (no) impact of a climate attribute on a biological response were based on our group knowledge of the literature. The severity of the impact was not considered, so minor impacts were considered equal to major impacts. Confidence scores were always lowest (1) for impact rating M (maybe) because we could not determine whether there would be a biological response to the climate attribute or not, most often because the interaction was either very complex or poorly studied, or both. For Y and N impacts, low confidence scores (2) reflected that we knew of few studies, or (3) some studies but poor literature consensus on the presence or absence of impact. Higher confidence scores (4) reflected multiple studies with some consensus, or (5) many studies with consistent findings that an impact would or would not occur. The number of Y impacts for each biological response was summed and median confidence in Y ratings was calculated across climate attributes to determine which biological responses might be most likely.

Level 2 analysis

Once Level 1 analysis determined that there were important general risks posed to biological processes by changes in short-term climate attributes, and which climate attributes contributed the most to this risk, Level 2 analysis focused on those risks in a more quantitative way in specific ecosystems. Below we outline three components of the analysis: first (under the heading "Climate-related risks") quantifying the potential severity of climate pressures in each ecosystem according to standardized criteria, and second (under the heading "Community Sensitivity") ranking biological sensitivity of each community using another set of criteria evaluating resilience to climate pressures based on life history characteristics. Finally, under the heading "Community vulnerability to climate risks in each ecosystem", we combine the results of the first two components to assess overall climate vulnerability across biological communities and ecosystems (Box 1).

Climate-related risks

After assembling data at the appropriate spatial and temporal scales for analysis, there were two steps to quantify climate-related risks: evaluating the probability that each anticipated climate effect would occur, and evaluating the severity of each effect relative to defined baseline conditions. We refined the list of anticipated climate effects from the Level 1 analysis and evaluated each effect by analysing existing quantitative information sources for the MAB and GOM ecosystems in Level 2 analysis (climate effects analysed are listed in Table 1, and a detailed list of climate time-series data sources are presented in the Appendix).

We developed standardized rating criteria to evaluate the probability of occurrence for each anticipated climate effect in the MAB, GOM, and in the full NE shelf region where ecosystem-level data were unavailable. Using a qualitative scale that combined existing observations and model predictions, low probability of occurrence (1) was assigned when no models predicted the change and there were no observations of the change, moderate to high probability (2–3) was assigned when models predicted the change, and very high to certain probability of occurrence (4–5) was assigned when the change was both predicted by models and already observed in the system. Category 0 indicated no probability of occurrence (Table 1).

Severity of each anticipated climate effect was then evaluated semi-quantitatively using four components: the degree of recent change relative to baseline caused by the effect, the duration of the effect, the recent trend of the effect, and the spatial scale of the effect. We used the last 5 years of each time series to characterize recent change (2006–2010). Baseline conditions were defined for each climate effect as those observed in the years 1960–1990, the same baseline years used in the Northeast Climate Impacts Assessment (NCIA, 2006). Criteria for scoring each component of severity are listed in Table 1, and further details on evaluating the time series according to these criteria are presented in the Appendix. Finally, we combined the four components of severity (degree, duration, trend and scale) into a single rating by averaging across the component ratings rescaling to the overall proportion of maximum possible severity.

To evaluate the relative importance among the climate attributes separately from any biological interactions, we plotted the probability scores against the combined severity scores; those attributes with both high probability and high severity are likely to pose the greatest risks to biological communities and ecosystem services. Finally, to assess the overall risk of each climate attribute in each ecosystem, we multiplied the probability by the severity scores and rescaled to the per cent of maximum possible, ranking the risk posed by each climate attribute on a scale from 1 (low, $<25\%$ of maximum) to 4 (high, $>75\%$ of maximum). These overall risk rankings were used to evaluate exposure to climate risks for biological communities, as described below.

Community sensitivity

We evaluated community sensitivity by looking at a specific set of community attributes to examine biological and ecological processes at risk of changing due to climate effects. Here, we adopt the framework which has been proposed for use in a more detailed species-level analysis for the full NE shelf region (M. Nelson, W. Morrison, R. Griffis, J. Howard, and J. Hare, pers. comm.). The general approach follows that of Chin *et al.* (2010) in evaluating the sensitivity of ecosystem residents based on their life history and degree of specialized biological characteristics. The sensitivity attributes include habitat and prey specificity, sensitivity to temperature and ocean acidification, complexity in reproductive strategy, larval settlement requirements, stock status, other stressors, population growth rate, dispersal of eggs and larvae, adult mobility, and temporal extent of spawning cycle. For each attribute, specific criteria were used to rank biota from high (4) to low (1) sensitivity, where animals with highly specialized biological attributes were considered more sensitive (criteria are listed in Table 2). Most sensitivity attributes could be ranked based on general life history information, but stock status relative to fisheries sustainable yield criteria was not always known, especially because we considered non-target species. Therefore, following a precautionary approach, groups with no information on stock status were scored high sensitivity (4), similar to stocks with known status less than half stock size at maximum sustainable yield. With the information available at the level we conducted the analysis, no other sensitivity attributes required an "unknown" score.

Because this assessment is intended to be rapid and preliminary, we assessed communities as aggregates rather than applying the analysis to each individual species and aggregating those results, a more time-consuming process (see Chin *et al.* (2010) and Doubleday *et al.* (2013) for examples of individual species-based risk assessment applications). However, because we are comparing the MAB and GOM, the species comprising the communities are different between the two ecosystems, and therefore have slightly different sensitivity characteristics. We first compiled lists of the major species in each of the six community groups (both commercial and non-target groups in each of three habitat categories: pelagic fish, demersal fish, and benthic invertebrates) in each ecosystem. Communities in each ecosystem were roughly as defined in Link *et al.* (2006); a list of representative species is included in the Appendix (Table A1). We then used our consensus expert opinion to assign qualitative sensitivity rankings for the aggregate species groups in each ecosystem, based on the characteristics of the major species comprising the group. General data quality scores were also assigned for each ranking. Scores for individual sensitivity attributes were combined by averaging across attributes (in this analysis, all attributes were equally weighted). While we did not attempt a full sensitivity analysis of this scoring system to determine its robustness to scoring errors, we found that changing a single attribute score by 1.5 points in either direction changed our overall sensitivity

Table 1. Anticipated climate changes, and criteria for evaluating their probability and severity, where s.d. is standard deviation of the time series in the reference period, 1960 – 1990, and recent years are the 5 most recent years in the time series.

	Criteria for evaluating anticipated changes					
		Criteria for evaluating 4 components of severity				
Anticipated climate change	**Probability of occurrence**	**Degree**	**Duration**	**Trend**	**Spatial scale**	**Confidence**
Temperature Warmer surface temp Warmer bottom temp Increased warm water thermal habitat volume (12-23C)	0. None: no evidence of change from modeling or observation.	(If prob of occurrence is 0, do not rate)	(If prob of occurrence is 0, do not rate)	(If prob of occurrence is 0, do not rate)	(If prob of occurrence is 0, do not rate)	0. None: change has never been investigated.
Hydrography Change in prevailing winds Rising sea level	1. Low: change not predicted by most models, no observations.	1. Low: change within 1 s.d. of baseline	1. Low: change present <33% of recent years	1. Low: no trend or current trend returning toward baseline	1. Low: change affects <33% of the area	1. Low: little scientific information to support ratings
Shifts in major boundary currents (Gulf Stream, Labrador Current)	2. Moderate: change predicted by some models but not others, few observations.	2. Moderate: change above 1 s.d. of baseline	2. Moderate: change present 33-66% recent years	2. Moderate: Non significant recent trend away from baseline	2. Moderate: change affects 33-66% of the area	2. Moderate: some information to support ratings, but conflicting
Salinity Fresher surface salinity Fresher bottom salinity **Mixing** Impeded vertical mixing	3. High: change predicted by majority of models, with supporting observations.	3. High: change above 2 s.d. of baseline If no s.d. (Sea level data), low 33% above worldwide average, moderate 33- 66% above, high >66% above.	3. High: change present >66% of recent years	3. High: Significant recent trend away from baseline	3. High: change affects >66% of the area	3. High: much information supports ratings with few conflicts
Increased riverine H2O inputs **Oxygen** Lower dissolved oxygen **Acidity** Increased acidity	4. Very high: change has been observed in a majority of the past 5 years, or is projected by most models.					4. Very high: well observed phenomena, no conflicting scientific information
Weather Increased storm frequency Increase storm intensity **Cumulative** Change in seasonal timing: Earlier spring	5. Certain: change has been consistently observed in system for past 10 years and is projected to continue by all models.					

Table 2. Criteria for ranking relative sensitivity of fish communities, based on attribute definitions to be used in a national climate vulnerability assessment protocol modelled on (Chin *et al.*, 2010) (M. Nelson, W. Morrison, R. Griffis, J. Howard, and J. Hare, pers. comm.).

	Criteria for ranking sensitivity levels			
Sensitivity attributes	**High sensitivity (4)**	**Moderate–high (3)**	**Low–moderate (2)**	**Low sensitivity (1)**
Habitat specificity	Restricted specialist	Specialist abundant hab	Particular pref	Generalist
Prey specificity	Specialist, no prey switching	Preferred single prey, switching detrimental	Limited number of prey types	Wide range
Sensitivity to ocean acidification	Shelled	Reliant on shelled spp	Somewhat reliant on shelled spp	Not reliant on shelled spp
Complexity in reproductive strategy	4+ characteristics	3 characteristics	2 characteristics	Simple
Sensitivity to temperature	Very limited range (1 province, one depth band)	Limited range	Moderate range	large range
Early life history survival and settlement requirements	Very specific larval requirements	Specific larval requirements	Minimal or unknown for larval	Minimal for larval
Stock size/status: B/Bmsy	<0.5 or UNKNOWN	>0.5 <0.8	>0.8 <1.5	>1.5
Other stressors (pollution, disease, foodweb impacts, etc.)	High (>3)	Moderate (2)	Limited (1)	Fishing only
Population growth rate	K selected, late maturing, long lived, low M	More towards K selected	More towards r selected	r selected, fast maturing, short lived, high M
Dispersal of early life stages: eggs and larvae	Minimal	Low	Moderate	Highly dispersed
Adult mobility	Non-mobile (sessile)	Ltd mobility, site dependent	Mobile but site dependent	Non-site dependant
Annual spawning events	Single narrow event	Confined time frame	Several events	Continuous spawning throughout year

score by <0.2. Therefore, we considered group scores different if they exceeded 0.2 points to account for potential single attribute scoring errors.

Community vulnerability to climate risks in each ecosystem

To assess exposure of each biological community to the climate risks analysed above, we applied a community-specific weighting scheme to the overall climate risk scores for each ecosystem. In general, the anticipated climate effects may apply more to a given habitat within an ecosystem, such that the impacts of climate change would be different on demersal, pelagic, and benthic organisms. For example, pelagic communities might be affected more by changes in surface conditions, while demersal and benthic communities would be more prone to changes at the bottom. We assigned weights to each climate attribute accordingly (a complete tabulation of weightings for each community and climate attribute is presented in the Appendix, Table A4). Overall exposure scores for each community in each ecosystem were calculated by averaging across the weighted climate attributes. We then plotted the overall exposure scores vs. the overall sensitivity scores for each community in the MAB and GOM to visually evaluate which communities were most vulnerable to the most likely short-term climate changes in each ecosystem (i.e. those with both high sensitivity and exposure).

Results

Level 1 analysis

Perhaps intuitively, animals' distribution range and centre were rated most likely to be affected by the most climate-driven changes with moderate to high confidence, followed by population productivity and phenology (Table 3). However, we are most confident that two climate pressures—warmer water and changing water chemistry (including salinity, dissolved oxygen (DO), and pH)—will affect animal physiology. Very few climate pressures were thought to have no impact on biological processes, and with low confidence: we judged changes in thermal habitat volume to have no direct impacts on productivity and physiology, and invading species to have no direct impacts on physiology and phenology, although it is possible to conceive of indirect impacts of these drivers on these processes (hence the low confidence rating). We had only low to moderate confidence in our ability to determine whether and how climate pressures would alter the ecological context (predator–prey interactions, competition, etc.). These detailed interactions are difficult to assess without more focused analysis and/or modelling that would be conducted in a Level 2 or higher risk assessment (e.g. Level 3 in Hobday *et al.* (2011)).

Level 2 analysis

Climate-related risks

A fairly simple standardized analysis of existing climate data time series revealed differences in potential severity of short-term climate risks between two distinct NE shelf ecosystems, the MAB and GOM. Climate time-series data reported in the Ecosystem Status Report (EcoAP, 2012) show higher variability overall in the MAB than in the GOM during the baseline years, approximately equal numbers of significant recent trends between regions, and more contrast in conditions between recent years and baseline years for the GOM (Figure 2). Recent surface temperatures in both ecosystems (and in the NE shelf in general) are above 1 s.d. of the baseline mean temperature; however, recent trends are opposite between the regions with continued increases in the GOM and a decrease towards the baseline in the MAB. In the GOM, recent bottom temperature was also above 1 s.d. of the baseline mean, perhaps because there was so little variation during the baseline years, while in the MAB there has historically been a wider range of both surface and bottom temperature variation. Surface and bottom salinities show similar patterns between the two regions,

Table 3. Level 1 analysis results.

	Anticipated effects of climate change in the Northeast US continental shelf region														Summary results	
Biological attributes of marine organisms	**Water temp increase**		**Volume of thermal habitat**		**Shifting hydro-grapy locally**		**Changing large-scale physical features**		**Changing water chemistry**		**Changing primary production (volume, timing)**		**New native or invasive species**		**Number "Yes" impacts**	**Median confidence in "Yes"**
Productivity	Y	4	N	2	M	1	M	1	Y	4	Y	5	Y	3	4	4
Physiology	Y	5	N	2	M	1	M	1	Y	5	M	1	N	2	2	5
Phenology	Y	4	M	1	Y	3	Y	3	M	1	Y	4	N	2	4	3.5
Ecological context	M	1	M	1	M	1	M	1	Y	3	Y	3	Y	3	3	3
Distribution range	Y	5	Y	4	Y	3	Y	3	Y	3	M	1	M	1	5	3
Distribution center	Y	5	Y	4	Y	3	Y	3	Y	2	M	1	M	1	5	3

Cells contain expert opinion-based impact ratings (Y = yes, M = maybe, N = no) and confidence scores (1 = none, 2 = low, 3 = moderate, 4 = high, 5 = very high) for impacts of anticipated climate-driven changes (columns) on generalized marine organism biological attributes (rows). See the text for more detailed descriptions of the biological attributes and anticipated climate effects.

with a higher range of baseline variability in the MAB and no clear departures from that range in recent years, in contrast to the narrower range in the GOM and a clearly declining trend in recent years for bottom salinity. Additionally, we see high recent river discharge and stratification in the GOM, with stratification exhibiting an increasing trend as well; comparable time series for the MAB showed considerable baseline variability but fairly flat recent trends near the baseline mean. There were significant recent trends in windstress and large-scale currents in the MAB as well as in the GOM (Figure 2). The comparisons of recent means, trends, and number of years above the mean in the last 5 years of each of these time series led to the ratings for each component of severity. Further details for all anticipated climate effects are summarized in the Appendix, and all ratings are in Table A2.

Combining the ratings on probability and severity for each of these climate attributes provides a picture of the relative risk posed by each at the full NE shelf, and at the MAB and GOM ecosystem scales (Figure 3). Attributes with both high probability and high severity appear in the upper right corner of Figure 3, so these represent the greatest short-term risks according to this analysis. We first note that all the identified climate attributes have at least a moderate probability of occurrence in the next 5–10 years because we started with a list that was appropriate to this region—a more generalized list may have contained attributes with low or no probability of occurrence (e.g. "changes in sea ice"). More important, nearly all the climate attributes were rated moderate or higher severity; only low DO, more winter storms, and more intense storms had relatively low severity ratings. Increased surface water temperature coastwide and sea-level rise were rated certain climate impacts because they are already observed consistently, while increased surface water temperature coastwide and in the GOM, and increased stratification in the GOM were among the most severe impacts examined. While multiple high-risk climate attributes are apparent in both ecosystems, there appear more high-risk climate attributes in the GOM than in the MAB. Combining probability and severity into a single index reinforces that both ecosystems have multiple moderate- to high-risk climate attributes for the next 5–10 years, but that there are more in the GOM relative to the MAB (Table 4).

Community sensitivity

We found the most contrast in the sensitivity of biological communities to climate change between habitat groupings, some contrast between ecosystems for certain groups, and almost no contrast between commercial and non-target status (Table 5). Benthic invertebrates were rated most sensitive, followed by demersals and then pelagics, regardless of commercial status. The high ranking of benthic invertebrates arose from the high sensitivity attributed to a combination of habitat specificity, lack of adult mobility, specific larval settlement requirements, and having calcareous shells (i.e. sensitivity to acidification). Conversely, pelagics were ranked least sensitive due to high adult mobility, low habitat specificity, and generally lower ratings across many other attributes than demersals or benthic invertebrates, regardless of ecosystem or commercial status. Within habitat groups, two groups had scores differing by at least 0.2 between ecosystems: commercial demersals and non-target benthic invertebrates were both rated more sensitive in the MAB, reflecting the different representative species used for each community. MAB commercial demersals have more complex life histories than GOM species, increasing sensitivity, while MAB non-target benthic invertebrates include more acidification-sensitive species such as corals. The only potential difference in sensitivity

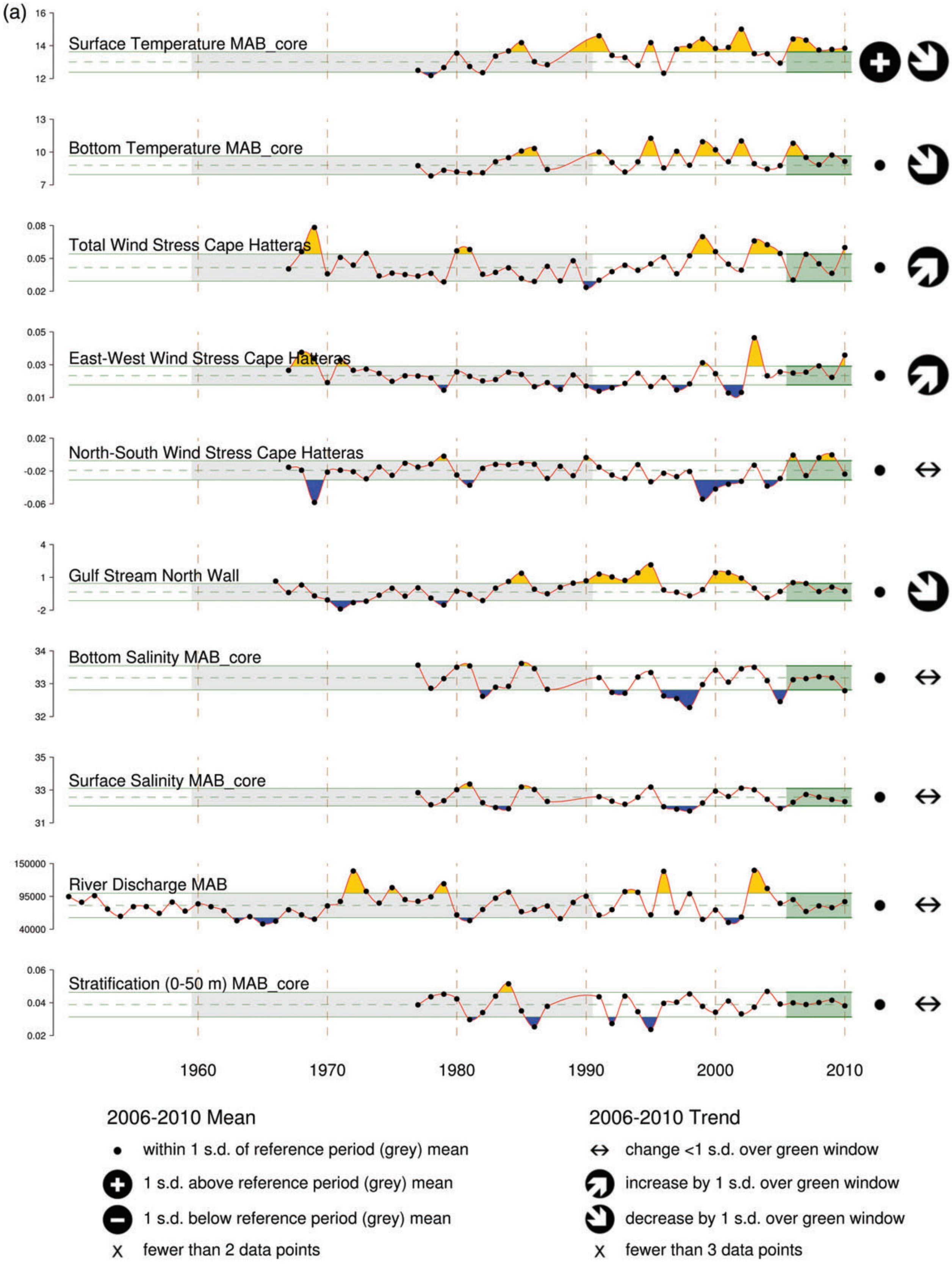

Figure 2. (a) Mid Atlantic Bight (MAB) climate attributes, and (b) Gulf of Maine (GOM) climate attributes. Grey shading = reference period, 1960 – 1990, green shading = recent period for comparison, solid green lines ±1 s.d of reference period mean (dashed green line).

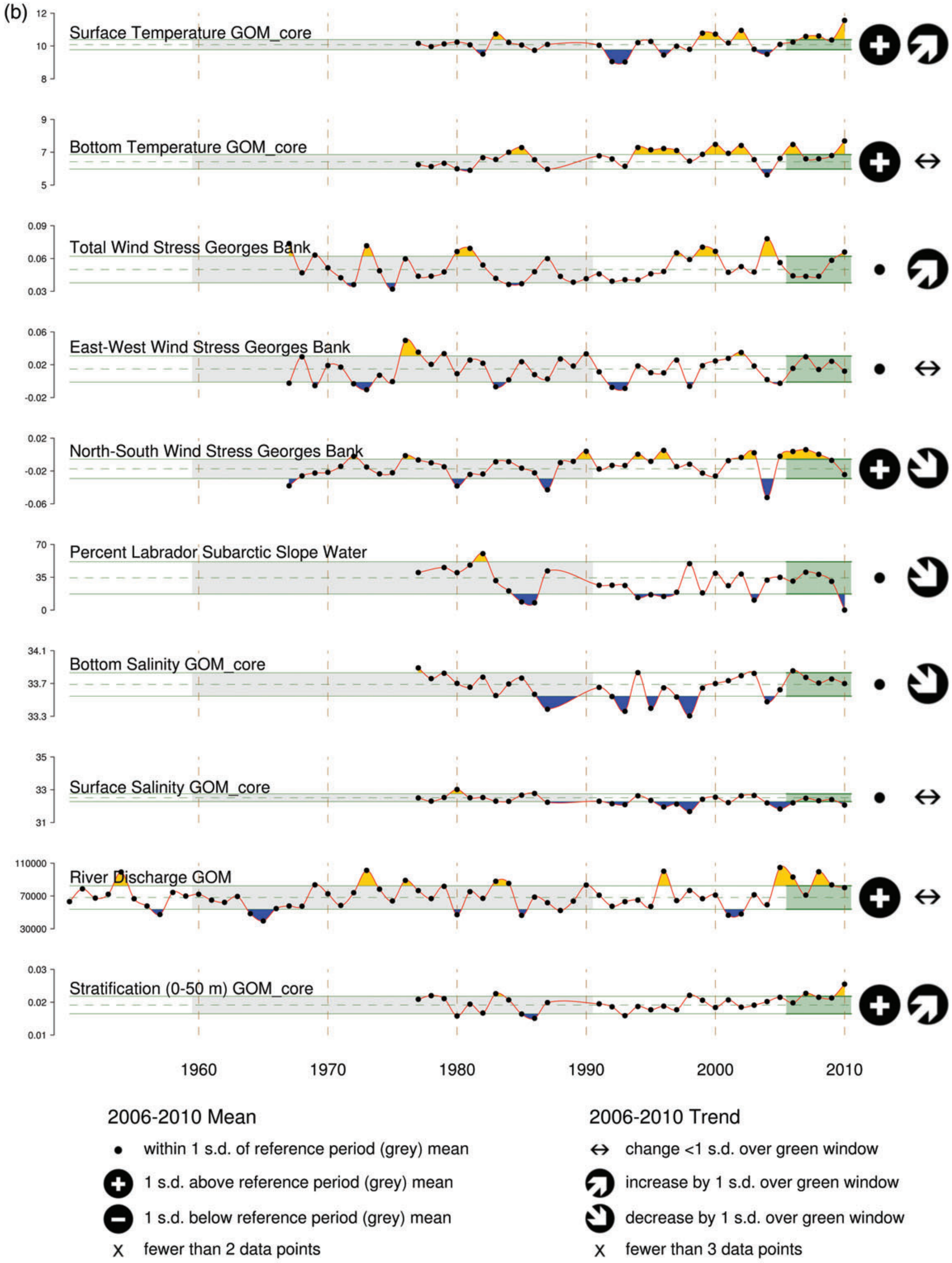

Figure 2. (Continued).

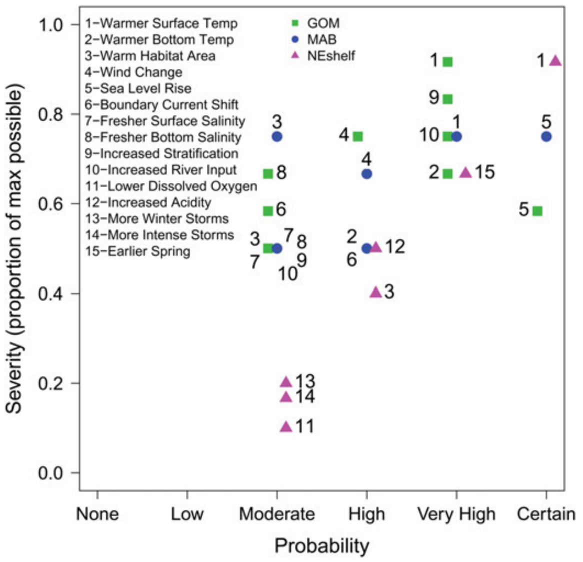

Figure 3. Overall 5 – 10 year risks posed by each climate attribute from Level 2 analysis. Probability vs. severity scores (rescaled) for each climate attribute, by region (Mid Atlantic Bight (MAB) and Gulf of Maine (GOM)).

Table 4. Level 2 analysis results.

Climate pressure attributes	MAB	GOM
Increased temperature—surface	3	3
Increased temperature—bottom	2	3
Increased warm thermal habitat	2	1
Change in prevailing winds	2	2
Sea level rise	3	3
Boundary current shift	2	1
Decreased salinity—surface	1	1
Decreased salinity—bottom	1	2
Increased stratification	1	3
Increased river input	1	3
Decreased DO	1	1
Increased acidity	2	2
More winter storms	1	1
More intense storms	1	1
Earlier spring	3	3

Combined probability × severity scores (5 – 10 year time horizon) for climate pressure attributes for the MAB and GOM from lowest (1) to highest (4) risk. Numeric categories are based on the % of the maximum possible Probability × Severity (0 – 25% of max = 1, >25 – 50% of max = 2, >50 – 75% of max = 3, >75% of max = 4).

Table 5. Level 2 analysis results.

	Mid Atlantic Bight	Gulf of Maine
Commercial pelagics	2.0	1.96
Non-target pelagic	2.08	2.08
Commercial demersals	2.58	2.25
Non-target demersals	2.5	2.38
Commercial benthic invertebrates	3.0	2.83
Non-target benthic invertebrates	3.29	2.96

Ranking community sensitivity across all attributes, where 1 = lowest and 4 = highest overall sensitivity. We considered scores differing by >0.2 to be likely to represent different levels of sensitivity.

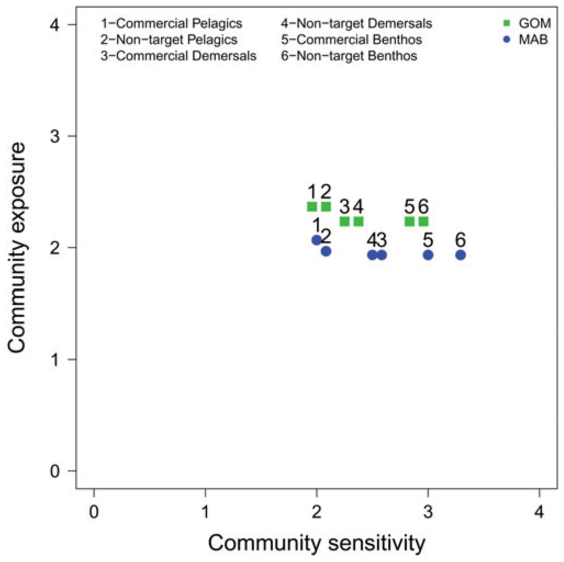

Figure 4. Community vulnerability to climate risks over the next 5 – 10 years from Level 2 analysis. Sensitivity vs. exposure (rescaled) in each region (MAB and GOM).

between commercial and non-target species within a habitat group was for benthic invertebrates in the MAB, again due to the sensitivity of corals. A full set of rankings with data quality (uncertainty) scores is presented in the Appendix, Table A3.

Community vulnerability to climate risks in each ecosystem

Combining the community sensitivity and climate risk analyses, we can identify the most and least vulnerable communities in each of the MAB and GOM ecosystems to the likely short-term climate attribute changes expected in each ecosystem. While some MAB communities had higher sensitivity, GOM communities had higher exposure to climate risks based on the analysis presented above (Figure 4). Community exposure resulted from the single index of climate risk combining probability and severity for each ecosystem (Table 4) weighted appropriately for each community (Appendix, Table A4). Figure 4 identifies the most vulnerable communities as those with the highest sensitivity and exposure in the upper right-hand section of the plot. Overall, pelagics had slightly higher exposure but lower sensitivity than demersals or benthos in this assessment due to clear increased surface temperature signals in both ecosystems, while benthic invertebrates were highly sensitive with roughly equal exposure to climate risks within an ecosystem as demersals.

Discussion

We draw two primary conclusions from this exercise, addressed in two sections below. First, we discuss the implications of this risk analysis for the Northeast US, including the big picture of climate risks in the region and impacts to the biological communities. We also discuss data gaps and needs revealed by the assessment, and finally some management implications for the region. Second, we outline the key attributes of risk assessment in general that make it a valuable tool to address the myriad "other conditions" of Hjort that influence fishery fluctuations.

Regional implications of this assessment

The Northeast US shelf region is currently exhibiting clear signals of a changing oceanographic system related to climate (EcoAP, 2012). It is projected to continue to do so in the near and long-term future (Hare *et al*., 2010, 2012). Beyond simply the typical thermal indicators, many measures demonstrate that this ecosystem is changing consistent with expectations associated with climate change (e.g. Nye *et al*., 2009; Pinsky and Fogarty, 2012). Apart from trends and long trajectories, a key observation is the physio-chemical environment of this ecosystem has become more variable interannually (Friedland and Hare, 2007). Our focus on many regional, fishery-relevant climate data time series over recent history suggests that this dynamic environment may impact fisheries resources over the next 5–10 years; therefore, there is a risk that fishery management objectives (i.e. sustainable yield, population rebuilding) will not be met unless these changing conditions are considered.

Our analysis indicates which fish and invertebrate communities of the NE shelf region are likely to be most vulnerable to the effects of climate change. Particularly sensitive are those animals that are less mobile, dependent upon calcium carbonate, and associated with specific habitats. The benthos in both the MAB and GOM were more vulnerable than other groups. Changes in the physio-chemical environment can impact these communities via a wide range of mechanisms (Brander, 2010; Pörtner and Peck, 2010), and the vulnerability is present and projected to persist. We note that there were several potentially important physical changes that we were unable to address with current information. Aside from overall changes in sea level, measurements of change in local hydrography were not readily available for comparative assessment between the MAB and GOM, and the NE shelf region as a whole needs better information on smaller scale hydrography and habitat changes, nutrient inputs, and ocean acidification. We further note that our analysis focuses on the short-term but that the long-term impacts must be kept in mind, and may arise from the climate attributes considered lower risk in the short term as well as those identified as high risk. However, specific long-term impacts may be difficult to assess as global climate models are not designed to provide regional or short-term predictions (Stock *et al*., 2011).

Despite these caveats, our analysis makes it clear that the exposure of the fish and invertebrate communities of the NE shelf region is slightly higher in the GOM than the MAB, largely due to the additional climate risks from decreasing salinity, increasing river discharge, and stratification, while both ecosystems have increasing temperature and changing wind and current patterns. These distinctions aside, all the communities we examined face moderate to high relative risk of climate impacts. In fact, demonstrable climate impacts have already begun to be documented for individual species in this ecosystem (Weinberg, 2005; Hare *et al*., 2010, 2012; Nye *et al*., 2011).

The risk analysis we have shown here provides one means for focusing, and perhaps prioritizing, where more detailed species-specific analysis, Level 3 risk evaluations, or refined stock assessments should occur. Our analysis suggests the following priorities for monitoring and management in each ecosystem (which are under the jurisdiction of separate fishery management entities). In both ecosystems, the high sensitivity of benthic invertebrates suggests increased monitoring and assessment priority, especially because bivalves and lobsters currently support the most economically important commercial fisheries in each region (Lowther, 2013). In the more variable MAB, there are less clear climate change signals in the immediate future but potentially a more sensitive set of species. This suggests that increased monitoring for climate impacts (in particular from increased water temperature and near-shore habitat loss due to sea level rise) to the most sensitive groups is warranted. In contrast, the GOM's clearer and more severe short-term climate risks combined with somewhat sensitive species suggests that management might need to change in the near term, in addition to increasing monitoring for climate impacts (warming, freshening, increased stratification) on sensitive species. The recent request by the New England Fisheries Management Council to consider current climate conditions explicitly in groundfish stock reference points (NEFMC, 2013) demonstrates a step towards altering management based on climate, and further assessment of climate risk to individual species could help prioritize which reference points are developed first. Another potential analysis for both ecosystems could identify threshold normal ranges of the climate change attributes most likely to affect communities, and use these ranges to identify when the system goes beyond previously observed conditions, perhaps triggering more conservative management actions for all species.

We note that a comparable evaluation of risk for some of the demersal fish communities in the NE shelf region (Patrick *et al*., 2010) with respect to fishing also indicated a moderate to high risk for species throughout the region, in addition to the moderate to high climate-related risk we have identified. Although not assessed here, the cumulative risk to these communities from both climate and the history of high fishing pressure (e.g. Link *et al*., 2011) raises several important more general issues. Overall, multiple stressors suggest a greater risk of negative events potentially impacting these fish communities. There will likely be unaccounted for dynamics and perhaps unintended consequences of well-meaning but overly narrow management for these fishery communities. For example, management strategies that limit fishers to catching certain species in certain ecosystems may not work under the shifting species distributions and community dynamics of climate change. Similarly, interactions of fishery species with protected species may change as distributions shift, requiring more integrated assessment to avoid negative impacts to both groups and to fishers. Therefore, the need for mitigating both fishing and climate impacts suggests considering more factors in assessment than in a routine fisheries management context, and adopting precautionary approaches, perhaps invoking atypical harvest control rules and more adaptive management considering a wider range of options when managing these communities. For example, allowing fishers to sustainably exploit "new" species shifting from other management jurisdictions while traditional species shift away may mitigate some climate-driven economic and social impacts to fisheries (MCCIP, 2012; Pinsky and Fogarty, 2012). In addition, while our risk assessment addressed the 5–10 year time horizon relevant to immediate fisheries management, there will still be a need for assessment at longer time scales for development of more comprehensive alternative and adaptive management strategies. In all of these cases, some form of hierarchical ecological risk assessment should be considered as a first step to establish priorities for more detailed work (e.g. Pecl *et al*., 2011).

Risk assessment: a tool to prioritize Hjort's "other conditions"

Much important process-based, mechanistic, and associated analytical work has been completed demonstrating the impacts of global climate change on living marine resources (e.g. Ji *et al*., 2007;

Howell *et al.*, 2008; Talmage and Gobler, 2010). Further, there are quantitative analyses of the effect of climate change on resource species (Fogarty *et al.*, 2008; Hare *et al.*, 2010, 2012). Yet there is no feasible way that such detailed analyses can be executed for all stocks in the northeast US shelf region, and more broadly all species in all ecosystems found in the world's oceans. What we have shown here is that Level 1 or 2 risk analysis is a relatively practical, rapid and thus low cost alternative to the more detailed approaches, as have others (Fletcher, 2005; Hobday *et al.*, 2007; Smith *et al.*, 2007; Patrick *et al.*, 2010; Hollowed *et al.*, 2013). The risk analysis we demonstrate here is highly transparent, takes advantage of the plethora of existing data, and assembles a suite of information into comprehensive yet digestible format for researchers and managers alike. Given the need to address climate change issues affecting marine resources, this approach can help to prioritize the best issues to focus upon while providing reasonable coverage for a wider range of taxa. Certainly further steps such as executing more detailed climate risk and mitigation analyses where deemed necessary, developing operational objectives based on stakeholder values or management actions to meet those objectives, and doing so in an interactive management-policy context need to occur (see, e.g. Pascoe *et al.*, 2009; Dichmont *et al.*, 2013).

Finally, we return to Hjort and his "other conditions" to note how prescient he was 100 years ago. Clearly factors beyond fishing (such as pollution, habitat alteration, species interactions, and environmental variability) are important and indeed influence the fluctuation of marine stocks (Schaefer, 1956). There are many other conditions besides fishing that can impact the dynamics of stocks and they collectively need to be accounted. As has been noted repeatedly, ignoring these other factors no longer remain a viable option (Gaichas, 2008; Link, 2010). Risk assessment as demonstrated here provides a standardized and transparent framework for scientists and managers to begin to address these other conditions.

Acknowledgements

We are grateful to Kevin Friedland and John Manderson for providing revised ecosystem indicators of spring bloom timing and butterfish thermal habitat, respectively, for the NE shelf region. The general format for Figure 2 was developed at the NOAA NMFS Alaska Fisheries Science Center by Kerim Aydin, Stephani Zador, and S. Gaichas. The NOAA Fisheries rapid climate vulnerability assessment tool for fish stocks is currently in development by Mark Nelson, Wendy Morrison, Roger Griffis, Jennifer Howard, Jon Hare, Wes Patrick, Eric Teeters, Bill Arnold, Karla Gore, Mike Pentony, Tobey Curtis, Jonathan Phinney, Jon Brodziak, Paul Spencer, Brett Weidoff, Rusty Brainard, Nick Tolmeri, Rick Hart, Yvonne deReynier, and Josh Lindsay. This paper was inspired during a review of ecological risk assessment methods for integrated ecosystem assessment by the ICES Working Group on North Atlantic Regional Seas (ICES WGNARS), 28 January 28–1 February 2013, co-chaired by Catherine Johnson and S. Gaichas. Roland Cormier, M. Robin Anderson, and Pierre Pepin contributed reviews of ecological risk assessments from their regions along with S. Gaichas and J. Link. The full working group conducted an example Level 1 risk analysis for climate impacts on Georges Bank and Gulf of Maine cod during the meeting. The meeting report is available at http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGRSP/2013/WGNARS13.pdf. We are grateful for constructive reviews of this manuscript by Kevin Friedland and three anonymous reviewers, which greatly improved the presentation.

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Appendix: Details of Level 2 analysis

Methods

Climate time-series data sources: The most useful source of data was the Northeast Fisheries Science Center's Ecosystem Status Report (ESR) which compiles standard physical, climate, ecological, and social indicators every 2 years for four Ecosystem Production Units (EPUs) within the NE shelf region (EcoAP, 2012). To evaluate whether the anticipated changes in regional climate attributes listed for Level 1 analysis are being observed, and to what degree in specific ecosystems, we analysed ESR time series for water temperature (surface and bottom), large-scale wind patterns and ocean boundary currents, salinity (surface and bottom), river discharge, and stratification in the MAB and GOM. We also analysed time series of warm water (12–23°C) thermal habitat volume for the full shelf and ecosystems (J. Manderson, NMFS, pers. comm.) and for the timing of the spring bloom in the NE shelf region (K. Friedland, NMFS, pers. comm.). Other published values were used to evaluate relative rates of sea level rise in the MAB and GOM (Titus *et al.*, 2009), DO (Gilbert *et al.*, 2005; Diaz and Rosenberg, 2008; US EPA, 2012), number of winter storms (Hirsch *et al.*, 2001; DeGaetano *et al.*, 2002; NRCC, 2013), intensity of tropical and extratropical storms (Zhang *et al.*, 2000), and timing of spring (NCIA, 2006) in the entire NE shelf region. A proxy value from another North Atlantic marine ecosystem was used to evaluate potential rates of ocean acidification (Bates and Peters, 2007; Olafsson *et al.*, 2009), as no data were available for the NE shelf region. Although long-term changes have been documented in

Table A1. Representative species for each community, by ecosystem.

Community	Equivalent group in Link *et al.* (2006)	MAB representative species	GOM representative species
Commercially important demersals	Demersals—piscivores, omnivores, benthivores	Spiny dogfish Black sea bass Summer flounder Tilefish Croaker	Atlantic cod Pollock Redfish Witch flounder Silver hake Goosefish Thorny skate
Non-target demersals	Demersals—piscivores, omnivores, benthivores	Northern sea robin Some skates Smooth dogfish Ocean pout Flatfish Drums	Sea raven Longhorn sculpin Other gadoids
Commercially important pelagics	Small pelagics—commercial, squid	Atlantic herring Atlantic mackerel Butterfish Longfin squid Shortfin squid	Atlantic herring Atlantic mackerel Shortfin squid Hakes
Non-target pelagics	Small pelagic—other, anadromous	Myctophids Anchovies Silversides grenadiers	Sandlance Myctophids Grenadiers
Commercially important benthic invertebrates	Megabenthos—filterers (+ lobster), and Shrimp	Scallops Surf clams Quahogs Crabs	Lobster Northern shrimp
Non-target benthic invertebrates	Megabenthos-other (-lobster) and Shrimp	Horseshoe crab Other large crabs Sea stars Tunicates Sponges Other mollusks Corals	Other shrimps Large crabs Sea stars Tunicates Other molluscs

Table A2. Climate attribute probability of occurrence, severity (degree, duration, trend and spatial scale), and confidence for the MAB, GOM, and full NE shelf. Ratings scale from low to high: 0–5 for probability, 1–3 for severity components, and 1–4 for confidence; see criteria in Table 2.

Region	Climate attribute	Prob. of occurrence	Degree	Duration	Trend	Spatial Scale	Confidence
MAB	Warmer surface temp	4	2	3	1	3	4
	Warmer bottom temp	3	1	1	1	3	4
	Thermal habitat area (warm water species)	2	1	2	3	3	2
	Change in prevailing winds	3	1	1	3	3	2
	Rising sea level	5	3	2	3	1	4
	Shifts in major boundary currents (Gulf Stream)	3	1	1	1	3	2
	Fresher surface salinity	2	1	1	1	3	3
	Fresher bottom salinity	2	1	1	1	3	3
	Impeded vertical mixing (stratification)	2	1	1	1	3	3
	Increased riverine H_2O inputs	2	1	1	1	3	3
GOM	Warmer surface temp	4	2	3	3	3	4
	Warmer bottom temp	4	2	2	1	3	4
	Thermal habitat area (warm water)	2	1	1	1	3	2
	Change in prevailing winds	3	2	3	1	3	2
	Rising sea level	5	2	1	3	1	4
	Shifts in major boundary currents (Labrador)	2	1	1	2	3	3
	Fresher surface salinity	2	1	1	1	3	3
	Fresher bottom salinity	2	1	1	3	3	3
	Impeded vertical mixing (stratification)	4	2	2	3	3	3
	Increased riverine H_2O inputs	4	2	3	1	3	3
NES LME	Warmer surface temp (summer)	5	2	3	3	3	4
	Thermal habitat area (warm water species)	3	1	1	3	3	2
	Increased acidity	3	2	2	3	3	1
	Increased storm frequency	2	1	1	1	3	2
	Increase storm intensity (model predictions)	2	1	1	2	1	2
	Earlier spring (NECIA and bloom timing)	4	2	2	3	3	3
	Lower DO	2	1 (qualitative severity rating; no time series)				2

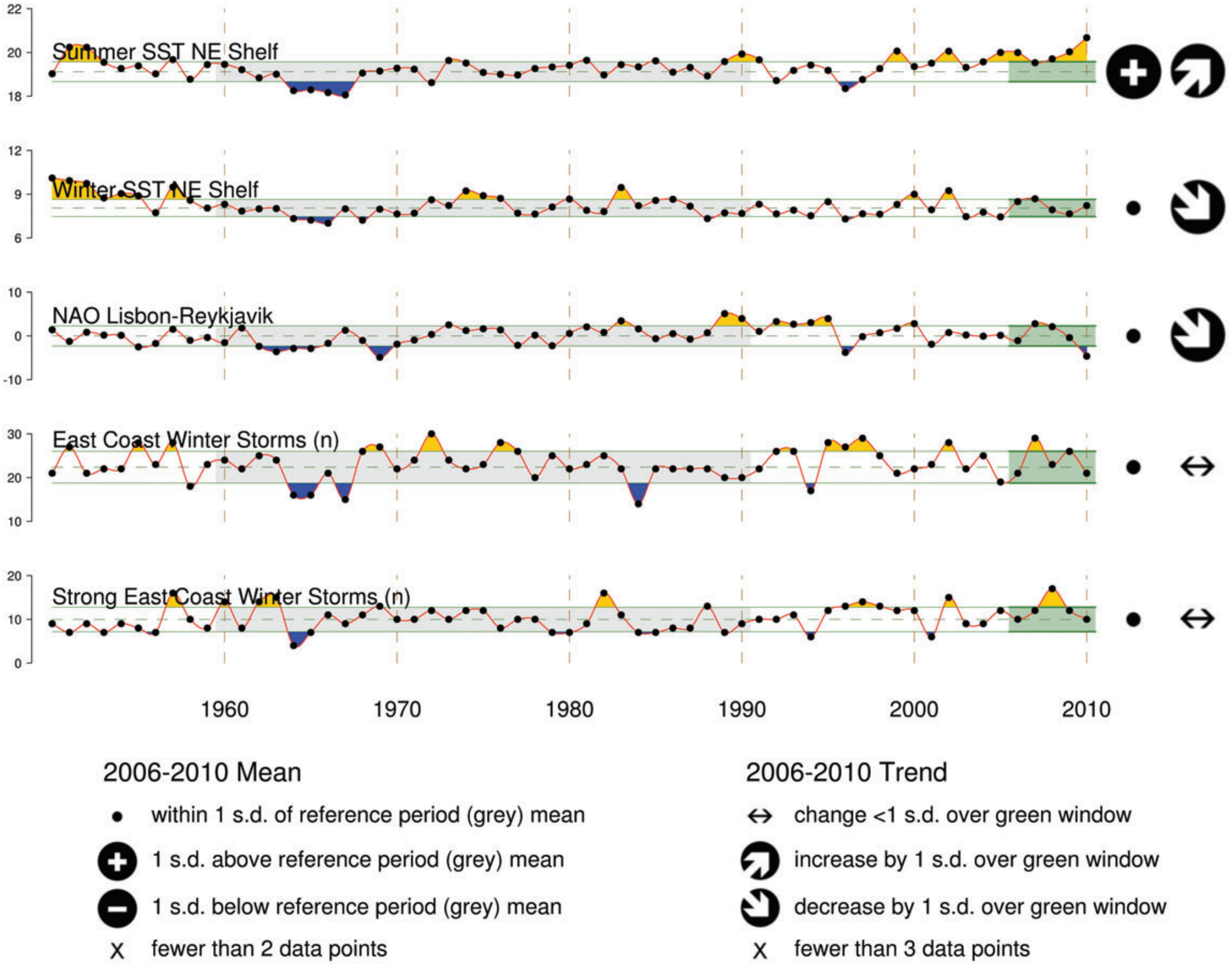

Figure A1. NE shelf-wide time series, same key as Figure 3.

other climatic variables in the region (e.g. in local current patterns, Smith *et al.* (2012), and nutrient inputs, Townsend *et al.* (2010)), annual-scale, long-term time series have not been compiled so these variables were not included in this analysis.

Severity component ratings: Criteria for rating degree, duration, and trend of effects were designed to compare the most recent 5 years of each available time series with the baseline conditions. We first calculated the mean and standard deviation of the baseline portion of each time series (all years with available data between 1960 and 1990). Lacking full short-term climate model projections for each climate attribute, we assumed that the short-term (5–10 year) future would be most likely to resemble the most recent past, and we considered 5 years to be the minimum number of data points for reasonable calculation of the following statistics. To evaluate degree of change, we calculated the mean of the most recent 5 year period and rated degree as low if the recent 5 year mean was within the standard deviation (s.d.) of the reference period, moderate if it was above 1 s.d. of the reference mean, and high if it was above 2 s.d. of the reference mean. Duration of the effect was the number of years in the most recent 5 with means exceeding 1 s.d. of the reference mean (1, low; 2–3, moderate; 4–5 high). Trend of the effect was evaluated by testing for a significant linear increase or decrease in the recent 5 years relative to 1 s.d. of the reference mean (low, no trend or trend back towards baseline; moderate, non-significant trend away from baseline; high, significant trend away from baseline). Spatial scale of an effect was qualitatively ranked as low, affecting <33% of the ecosystem's area, moderate, affecting 33–66% of the ecosystem, or high, affecting >66% of the ecosystem; we note that most of the time series from the ESR used data gathered at the full (>66%) ecosystem scale. We then combined the four components of severity (degree, duration, trend and scale) into a single rating by averaging across the component ratings rescaling to the overall proportion of maximum possible severity. We also rated scientific confidence in the overall effect.

Species groups: Representative species for each of the communities examined in the MAB and GOM ecosystems are listed in Table A1.

Results and discussion

Our full set of ratings for each climate attribute in the MAB and GOM ecosystems as well as for the entire NE shelf region are given in Table A2. In addition to the signals detected in the ESR time series for the MAB and GOM outlined in the main body of the text, there were also clear recent climate signals for the NE shelf as a whole. Summer surface temperature throughout the region is currently 1 s.d. higher than the baseline mean, with an increasing trend, but winter temperatures shelfwide show a decreasing recent trend

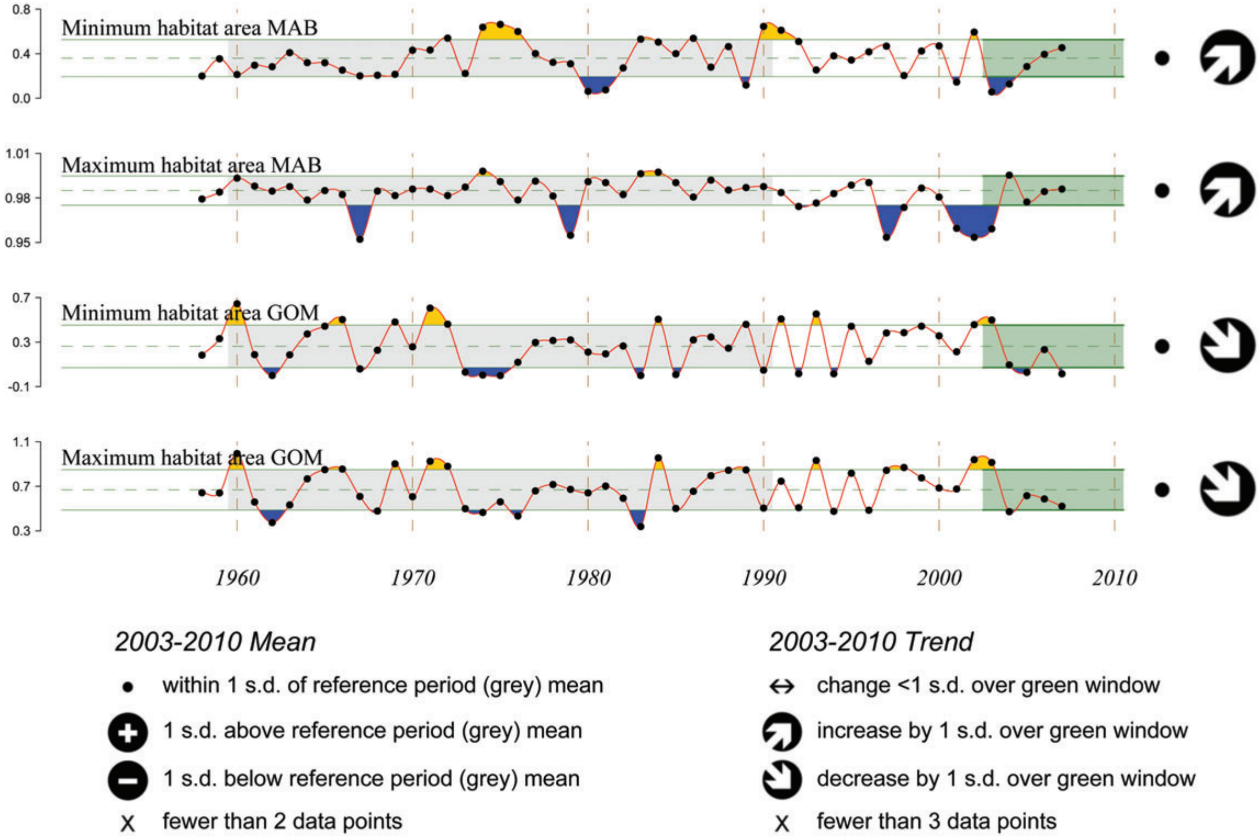

Figure A2. Thermal habitat indices, same key as Figure 3. Annual minimum and maximum warm water thermal habitat surface areas are expressed as a proportion of the annual maximum within each ecosystem.

(Figure A1). The North Atlantic Oscillation (NAO) shows a decreasing recent trend which may drive large-scale circulation changes throughout the coast that were observed for the two regions above. However, a long term dataset of NE shelf regional winter storms showed no recent trend relative to baseline for either the number of storms or the number of major storms (Figure A1). On land in the northeast US, spring (as defined by first plant budding or leafing out) has become increasingly earlier since the baseline years (NCIA, 2006). Spring bloom timing has also become increasingly earlier in recent years throughout the NES LME (K. Friedland, pers. comm.), although the time series do not extend back into the baseline period to make formal comparisons. Based on the two sources of incomplete information, we rated earlier spring moderate for degree and duration and high for trend and spatial scale, with moderate confidence. Ocean acidification data for the entire NES LME region are lacking; time series from other North Atlantic systems show steadily increasing acidification and decreased saturation of carbonates (Bates and Peters, 2007; Olafsson *et al.*, 2009). Based on this proxy data, we rated acidification moderate for degree and duration and high for trend and spatial scale, with low confidence.

Some additional information was available at the ecosystem scale that was not in the ESR. Thermal habitat for warm water species shows an increasing recent trend in the MAB, and a decreasing recent trend in the GOM (Figure A2). Sea level rise, which poses risks of coastal wetland and other nearshore nursery habitat loss or alteration for marine fish and invertebrates, is predicted to be a larger issue in the MAB than the GOM (Titus *et al.*, 2009). However, we judged the spatial scale of this impact to be limited to the coastal habitats (<33% of the area), so the overall severity remained similar comparing the ecosystems. Changes in DO are more difficult to assess between the two ecosystems; the MAB currently has more observed problems with coastal/estuarine hypoxia (driven by increased temperature and eutrophication) than the GOM (Diaz and Rosenberg, 2008; US EPA, 2012); however, these coastal issues also impact <33% of the total system area. On the continental shelves, DO levels may be more affected by changes in the relative influence of oceanic water masses (Gilbert *et al.*, 2005). Therefore, changes in the proportion of Atlantic (warmer, less oxygenated) water and Labrador (colder, more oxygenated) water in the GOM where the two masses mix may be very influential on oxygen concentrations there, while the MAB remains primarily influenced by the Atlantic water (EcoAP, 2012). However, assessments of coastal ocean water quality never found DO levels below the threshold where fish and benthos are affected, so this change was qualitatively rated as low severity overall in both ecosystems.

Our full set of community sensitivity scores are given in Table A3, and the weightings for exposure to climate risk by community for each ecosystem are given in Table A4.

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Table A3. Community sensitivity attribute scores, with data quality scores in italics.

Region	Community sensitivity attribute	Commercial pelagics		Non-target pelagics		Commercial demersals		Non-target demersals		Commercial benthic inverts		Non-target benthic inverts	
MAB	Habitat specificity	1.0	*2.0*	1.0	*1.0*	3.0	*2.0*	2.0	*2.0*	4.0	*3.0*	3.5	*3.0*
	Prey specificity	2.0	*3.0*	2.0	*2.0*	2.0	*3.0*	2.0	*2.0*	1.0	*3.0*	2.0	*2.0*
	Sensitivity to ocean acidification	2.0	*1.0*	2.0	*1.0*	2.5	*1.0*	3.0	*1.0*	4.0	*3.0*	4.0	*2.0*
	Complexity in reproductive strategy	3.0	*2.0*	2.0	*1.0*	3.5	*2.0*	2.5	*1.0*	2.0	*2.0*	3.0	*2.0*
	Sensitivity to temperature	1.0	*3.0*	2.0	*2.0*	2.5	*3.0*	2.5	*2.0*	3.5	*3.0*	4.0	*2.0*
	Early life history survival and settlement requirements	2.0	*2.0*	2.0	*1.0*	2.0	*1.0*	2.0	*2.0*	4.0	*2.0*	3.0	*2.0*
	Stock size/status: B/Bmsy	2.0	*2.0*	4.0	*1.0*	3.0	*2.0*	4.0	*1.0*	3.0	*2.0*	4.0	*1.0*
	Other stressors	4.0	*3.0*	3.0	*3.0*	2.0	*3.0*	1.5	*1.0*	3.0	*3.0*	3.0	*2.0*
	Population growth rate	2.0	*2.0*	2.0	*2.0*	3.0	*2.0*	3.0	*2.0*	2.5	*2.0*	3.0	*2.0*
	Dispersal of early life stages	2.0	*3.0*	2.0	*1.0*	2.5	*2.0*	3.0	*1.0*	2.0	*3.0*	3.0	*2.0*
	Adult mobility	1.0	*3.0*	1.0	*2.0*	2.5	*3.0*	2.5	*2.0*	4.0	*3.0*	4.0	*3.0*
	Spawning cycle	2.0	*2.0*	2.0	*1.0*	2.5	*2.0*	2.0	*2.0*	3.0	*2.0*	3.0	*1.0*
GOM	Habitat specificity	1.0	*2.0*	1.0	*1.0*	2.0	*2.0*	2.0	*2.0*	4.0	*3.0*	3.0	*3.0*
	Prey specificity	2.0	*3.0*	2.0	*2.0*	1.5	*3.0*	2.0	*2.0*	2.0	*3.0*	2.0	*2.0*
	Sensitivity to ocean acidification	2.0	*1.0*	2.0	*1.0*	2.0	*1.0*	2.0	*1.0*	3.5	*3.0*	4.0	*2.0*
	Complexity in reproductive strategy	3.0	*2.0*	2.0	*1.0*	2.0	*2.0*	2.0	*1.0*	2.5	*2.0*	2.5	*2.0*
	Sensitivity to temperature	1.0	*3.0*	2.0	*2.0*	2.5	*3.0*	2.5	*2.0*	3.5	*3.0*	3.0	*2.0*
	Early life history Survival and settlement requirements	2.0	*2.0*	2.0	*1.0*	2.5	*1.0*	2.0	*2.0*	3.0	*2.0*	3.0	*2.0*
	Stock size/status: B/Bmsy	2.0	*2.0*	4.0	*1.0*	3.5	*2.0*	4.0	*1.0*	2.5	*2.0*	4.0	*1.0*
	Other stressors	3.5	*3.0*	3.0	*3.0*	2.0	*3.0*	2.0	*1.0*	3.0	*3.0*	2.0	*2.0*
	Population growth rate	2.0	*2.0*	2.0	*2.0*	3.0	*2.0*	2.5	*2.0*	2.0	*2.0*	3.0	*2.0*
	Dispersal of early life stages	2.0	*3.0*	2.0	*1.0*	2.0	*2.0*	2.5	*1.0*	2.5	*3.0*	3.0	*2.0*
	Adult mobility	1.0	*3.0*	1.0	*2.0*	2.0	*3.0*	3.0	*2.0*	3.0	*3.0*	3.0	*3.0*
	Spawning cycle	2.0	*2.0*	2.0	*1.0*	2.0	*2.0*	2.0	*2.0*	2.5	*2.0*	3.0	*1.0*

Sensitivity ranges from 1 (low) to 4 (high); see Table 3 for rating criteria for each sensitivity attribute. Data quality ranges from 1 (low) to 3 (high).

Table A4. Exposure to climate risk weightings (default = 1) and weighted attribute scores; overall risk of attributes from Table 5.

Region	Climate pressure attribute	Overall risk	Commercial pelagics		Non-target pelagics		Commercial demersals		Non-target demersals		Commercial benthic inverts		Non-target benthic inverts	
MAB	Temperature—surface	3.0	1.5	4.5	1.5	4.5		3		3	.5	1.5	.5	1.5
	Temperature—bottom	2.0		2	.5	1	1.5	3	1.5	3	1.5	3	1.5	3
	Thermal habitat	2.0	1.5	3	1.5	3	1.5	3	1.5	3		2		2
	Prevailing winds	2.0		2		2		2		2	1.5	3	1.5	3
	Sea level rise	3.0		3		3		3		3		3		3
	Boundary current shift	2.0		2		2		2		2	1.5	3	1.5	3
	Salinity—surface	1.0	1.5	1.5	1.5	1.5		1		1	.5	0.5	.5	0.5
	Salinity—bottom	1.0		1	.5	0.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	Stratification	1.0	1.5	1.5	1.5	1.5		1		1		1		1
	River input	1.0		1		1		1		1		1		1
	DO	1.0		1		1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	Acidity	2.0		2		2		2		2	1.5	3	1.5	3
	More winter storms	1.0		1		1		1		1		1		1
	More intense storms	1.0		1		1		1		1		1		1
	Earlier spring	3.0	1.5	4.5	1.5	4.5		3		3		3		3
GOM	Temperature—surface	3.0	1.5	4.5	1.5	4.5		3		3	.5	1.5	.5	1.5
	Temperature—bottom	3.0		3		3	1.5	4.5	1.5	4.5	1.5	4.5	1.5	4.5
	Thermal habitat	1.0	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5		1		1
	Prevailing winds	2.0		2		2		2		2	1.5	3	1.5	3
	Sea level rise	3.0		3		3		3		3		3		3
	Boundary current shift	1.0		1		1		1		1	1.5	1.5	1.5	1.5
	Salinity—surface	1.0	1.5	1.5	1.5	1.5		1		1	.5	0.5	.5	0.5
	Salinity—bottom	2.0		2		2	1.5	3	1.5	3	1.5	3	1.5	3
	Stratification	3.0	1.5	4.5	1.5	4.5		3		3		3		3
	River input	3.0		3		3		3		3		3		3
	DO	1.0		1		1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	Acidity	2.0		2		2		2		2	1.5	3	1.5	3
	More winter storms	1.0		1		1		1		1		1		1
	More intense storms	1.0		1		1		1		1		1		1
	Earlier spring	3.0		4.5		4.5		3		3		3		3

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ICES Journal of Marine Science (2014), 71(8), 2343–2356. doi:10.1093/icesjms/fsu018

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Quo Vadimus

The future of fisheries oceanography lies in the pursuit of multiple hypotheses

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Hare, J. A. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. – ICES Journal of Marine Science, 71: 2343–2356.

Received 8 July 2013; accepted 19 January 2014; advance access publication 6 March 2014.

Fisheries oceanography is largely an applied discipline with a major goal of improving fisheries management and marine conservation. Johan Hjort's critical period hypothesis, and its decedents, remain a dominant theme and focuses on year-class success as mediated by prey availability and feeding. Bottom-up forcing, a related hypothesis, focuses on the sequential transfer of energy through the pelagic foodweb from primary productivity to fishery productivity. Another approach assumes that trophic interactions of adults determine abundance. Fisheries assessment and management, however, is based on the hypothesis that fishery abundance is determined by time-varying fishing and year-class success related to spawning-stock biomass. These approaches, their basic hypotheses, and underlying processes and mechanisms suggest very different dynamics for fishery populations. Other hypotheses challenge these traditional views: predation of early life stages, parental condition, shifting migration pathways, and physiological limits. Support for these other hypotheses is reviewed and the research needs are described to apply these hypotheses to fisheries assessment and management. Some of these hypotheses were identified by Hjort (e.g. parental condition hypothesis) and others are relative new (e.g. early life stage predation hypothesis). Moving into the future, we should focus on Hjort's approach: multi-hypothesis, integrative, and interdisciplinary. A range of hypotheses should be pursued with an emphasis on comparing and linking multiple hypotheses. The results then must be incorporated into fishery assessments and management decisions to support the long-term sustainability of exploited species and the conservation of threatened and endangered species.

Keywords: fisheries oceanography, fishery abundance, fishery distribution, Johan Hjort, multiple-hypotheses, population dynamics, recruitment, stock assessment, year-class success.

Introduction

Fisheries oceanography defined

Fisheries oceanography is defined as the study of oceanic processes that affect marine ecosystems and the relationship of these ecosystems to the abundance, distribution, and availability of fishery species (Harrison and Parsons, 2000; other definitions are summarized in Kendall and Duker, 1998). The emphasis is on exploited species, but fisheries oceanography includes species and processes that affect and are affected by exploitation. Species of interest include phytoplankton, zooplankton, finfish, shellfish, marine mammals, and sea turtles; processes of interest encompass the fields of oceanography, fisheries, and ecology. This essay treats fishery abundance and distribution. Availability to a fishery remains a relatively understudied facet of fisheries oceanography and involves an understanding of the interaction among the marine ecosystem, fishery populations, and fishing activities (e.g. gear-selectivity, socio-economics, fishing technology, regulation, etc.).

Basically, fisheries oceanography is an applied science with the potential to inform scientists, managers, and fishers. Many early researchers explicitly identified the applied aspects of their work as a main motivating factor (Hjort, 1914, 1926; Walford, 1938; Sette, 1943). Although "improving fisheries management" is stated as a goal in many fisheries oceanography studies, the direct connection to management is not often made. However, recent advances have brought us to the brink of widespread application of fisheries oceanography to fishery assessment and management (Köster *et al.*, 2003a, b). Also, the recognition of the need to manage fisheries in the context of the broader ecosystem

Published by Oxford University Press on behalf of the International Council for the Exploration of the Sea 2014.

(e.g. Ecosystem-Based Fisheries Management) brings fisheries oceanography to the forefront as a requirement for assessment and management (Rothschild, 1986; EPAP, 1999; Pikitch *et al.*, 2004; Cury *et al.*, 2008). In this essay, I track the development of fisheries oceanography, discuss the link between hypotheses and fisheries assessment, and suggest future directions for the field. In honour of Hjort's centennial, I provide an overview of the critical role of Hjort's hypotheses in the development of fisheries oceanography and advocate that we must embrace his approach, in addition to his hypotheses, to achieve the basic goal of improving fisheries assessment and management.

Johan Hjort sets the stage

Arguably, Johan Hjort is the father of fisheries oceanography. His 1914 and 1926 publications set the stage for a century of work aimed at understanding fluctuations in abundance of fishery species. Hjort knew that fishery yields varied through time, and his purpose was to understand the basis for this variability. He saw the potential to help fishers understand and respond to the natural dynamics of the resource and he even wrote about developing a predictive capability. His approach was hypothesis-driven (Table 1), and he brought a number of lines of evidence and tools to bear in his investigations. He also synthesized information from other researchers and from several stocks of both Atlantic cod and Atlantic herring. Hjort did not work in a vacuum and an excellent summary of the historical and scientific context of his work is provided by Sinclair (1997).

In total, Hjort considered two general hypotheses and three subhypotheses (Table 2). When Hjort began his work, the standing hypothesis was that variable fishery yields were caused by variable adult migration (H_1), which led to variable overlap with fishing effort; abundance varied relatively little (see Sinclair, 1997). Migrations were caused by seasonal changes in the environment (abiotic and biotic) and the sensitivities of adult fish to these changes. Through the investigations of Hjort and his contemporaries, the migration hypothesis was discounted. In its place, Hjort accumulated a large amount of evidence to support the hypothesis that fluctuations in fishery yields resulted from fluctuations in population abundance caused by variability in year-class success (H_2), defined as the number of individuals that survive early life stages (eggs, larvae, and juveniles) to join the adult population. Hjort acknowledged that the renewal of a fish stock was dependent on many factors and that poor conditions in any one factor could determine the ultimate result. However, he identified and discussed three subhypotheses regarding the determination of year-class success: (a) quality and quantity of spawning (H_{2a}), (b) nourishment of young larvae (H_{2b}), and (c) passive movement of larvae in currents (H_{2c}) (often termed Hjort's second hypotheses, Sinclair *et al.*, 1985). Based on examination of cod liver and roe, Hjort found the years with highest year-class success were correlated with the lowest roe weights and thus, he discounted the quality and quantity of spawning hypothesis (currently termed the parental condition hypothesis). With regard to the nourishment of larvae, he discussed the potential importance of starvation after hatch (the critical period hypothesis) and the timing of spawning relative to the timing of primary production (currently termed the match–mismatch hypothesis). He did not discuss the dispersal of larvae in detail but recognized the potential importance of passive and active movements to and from favourable conditions.

Since Hjort's publications, his first-feeding hypothesis (H_{2b}) received the most attention. From this research, many of the classic tenets of fisheries oceanography originated. The critical

Table 1. Definitions of hypothesis, process, and mechanism as used in this essay.

Hypothesis: A proposed explanation for a phenomenon that can be tested. In this essay, the phenomenon is variability in the abundance and distribution of fishery species

Process: An ecological action that reaches a particular effect. Five processes are identified here as causing variability in the abundance and distribution of fishery species: (i) prey/feeding, (ii) predation, (iii) movement/dispersal, (iv) ecophysiology, and (v) reproduction/spawning

Mechanism: A system of causally interacting parts that constitute a process in a specific case. For example, the mechanism of the parental condition hypothesis proposed by Friedland *et al.* (2008) consists of seven parts (Figure 3)

Table 2. List of hypotheses considered here.

Hypothesis	Source	Description
1. Migration/ movement	Hjort (1914)	Variability in migration pathways result in variability in availability to fisheries while adult abundance remains relatively constant; distribution varies as a result of variable movement (the stipulation that abundance is relatively constant is no longer part of the migration/ movement hypothesis)
2. Year-class success	Hjort (1914)	Variability in survival during prerecruit stages result in variability in adult abundance
2a. Parental condition	Hjort (1914)	Variability in parental investment in offspring results in variability in prerecruit survival
2b. Prey environment	Hjort (1914)	Variability in prey abundance and prey distribution results in variability in prerecruit survival
2c. Dispersal	Hjort (1914)	Variability in dispersal results in variability in prerecruit survival
2d. Predation	Bailey and Houde (1989)	Variability in predation results in variability in prerecruit survival
2e. Ecophysiology	Fry (1971), Neill *et al.* (1994)	Variability in the physiological environment results in variability in prerecruit survival
2f. Growth-mortality	Anderson (1988)	Variability in the interaction between growth and mortality results in variability in prerecruit survival
3. Fishing and recruitment	Beverton and Holt (1957)	Variability in survival during prerecruit stages and fishing mortality result in variability in adult abundance
4. Adult trophic interactions	Odum and Odum (1955), Polovina (1984)	Variability in adult prey and predation results in variability in adult abundance

The four general hypotheses are denoted by Arabic numerals and the six subhypotheses are denoted by letters. This notation is used throughout the text. This list is not comprehensive in terms of hypotheses that explain variability in the abundance and distribution of fishery species (see Figure 2 and Houde, 2008).

period hypothesis proposes that year-class success is determined by prey availability at the transition from yolk-sac to exogenous feeding (Hjort, 1914). The match–mismatch hypothesis proposes that year-class strength is determined by the match between prey production and spawning cycles of the focal species (Cushing, 1990). The stable ocean hypothesis proposes that ocean stability allows aggregation of larval prey, thereby enhancing feeding conditions and by extension year-class success (Lasker, 1978). Similarly, the optimal environmental window hypothesis states that year-class success is related to local optimal environmental conditions that maximize prey production (Cury and Roy, 1989). In general, these hypotheses are refinements of Hjort's original hypothesis and propose that the feeding environment of planktonic larvae is the dominant factor shaping year-class success and ultimately the abundance of fishery populations. There are examples that provide strong support for these prey-related hypotheses (e.g. Ringuette *et al.*, 2002; Castonguay *et al.*, 2008), but the support is not universal (May, 1974; Houde, 2008).

Over the past century, efforts to understand fluctuations in fishery abundance have not only focused on the larval feeding environment. Walford (1938) examined the retention of haddock larvae on George's Bank. This work followed Hjort's dispersal hypothesis (H_{2c}) and many others have examined this hypothesis (e.g. following Walford: Colton and Temple, 1961; Myers and Drinkwater, 1989; Boucher *et al.*, 2013). The role of larval dispersal in broader population dynamics was further developed in the member-vagrant hypothesis (Sinclair, 1988) and through studies of population connectivity (Pineda *et al.*, 2007; Cowen and Sponaugle, 2009). Like the larval feeding hypotheses, the larval dispersal hypothesis proposes that year-class success is a dominant component of fishery abundance but is determined by dispersal to favourable habitats for continuation of the life cycle rather than the larval feeding environment.

Towards forecasts of fishery abundance and distribution

Taking a step back from Hjort, four general hypotheses exist that explain fluctuations in fishery abundance (Figure 1 and Table 2). The first two hypotheses were dealt with by Hjort: movement/migration (H_1) and year-class success (H_2). The third is the standard fisheries hypothesis (H_3): recruitment is related to spawning-stock biomass and interannual changes in fishing mortality are responsible for changes in total mortality (Hilborn and Walters, 1992; Quinn and Deriso, 1999). The role of overfishing in declining fishery abundance was investigated during Hjort's time, but by a different group of scientists (see Sinclair, 1997). The fishing hypothesis assumes that year-class success is an important driver of fishery abundance (*sensu* Hjort) but does not try to understand recruitment variability beyond that explained by spawning-stock biomass; this variability is modelled simply as randomly distributed error in the stock–recruitment relationship. A population can be managed at a certain level, if a certain fishing mortality can be maintained. Recruitment can be measured by surveys, thus removing the need to understand the processes that cause variability in recruitment. The fourth hypothesis (H_4) is based on the transfer of energy through foodwebs (Odum and Odum, 1955; Polovina, 1984). Biomass of a given component of an ecosystem depends on food resources and predation pressures. This approach originated from ecological theory and has expanded greatly in the study of marine systems, which have been represented as food chains (e.g. Ryther, 1969) and foodwebs (e.g. Pauly *et al.*, 2000). This hypothesis focuses on trophic interactions of adult stages and ignores the complex life history of many marine species.

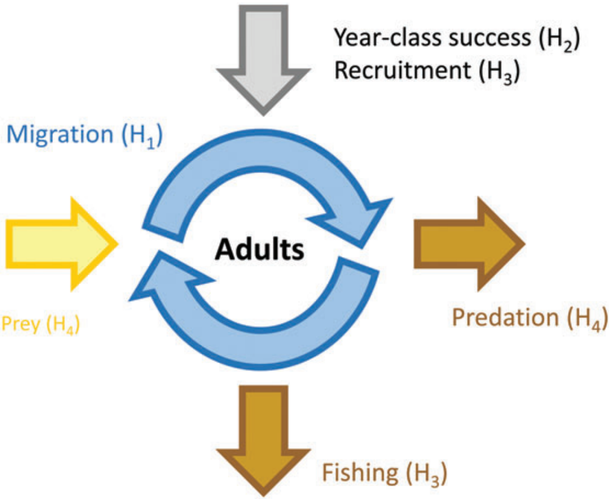

Figure 1. A schematic illustrating the four main hypotheses for variability in fishery abundance: (1) migration, (2) year-class success, (3) fishing and stock–recruitment relationship, and (4) adult trophic interactions. See Table 2 for a brief description of these hypotheses. The colours correspond to the main operating process of the hypothesis (Figure 2).

To further develop the applied aspects of fisheries oceanography, the differences between these four general hypotheses need to be recognized and links need to be made among their implied processes and mechanisms (Figure 1, Table 1). For example, over the past 25 years, a large amount of effort has gone into modelling the physical environment, primary productivity, and zooplankton productivity. Many of these models have been linked to fishery populations through larval feeding and larval dispersal (Werner *et al.*, 2001, 2007; North *et al.*, 2009; Hinrichsen *et al.*, 2011). At the heart of these models, often implicitly, is the hypothesis that variability in year-class success drives variability in population abundance (H_2). Further, variability in year-class success is determined by the larval feeding environment (H_{2b}) or larval dispersal (H_{2c}). Thus, these efforts are based on the classic hypotheses of recruitment fisheries oceanography (*sensu* Kendall and Duker, 1998). An important limitation to applying these oceanographic models is that they consider only a subset of the hypotheses that explain fishery abundance and distribution.

The issue of developing forecast and predictions based on narrowly focused models is not restricted to the investigation of year-class success. Similarly, limited examples could be provided for the remaining three general hypotheses identified as controlling fishery abundance (H_1, H_3, H_4). Fisheries oceanography, as defined above, is compartmentalized in terms of the hypotheses that are used to explain variability in fishery abundance and distribution. Oceanographers and ecologists focus on variability in year-class success (H_2), fishery assessment scientists emphasize the stock–recruitment relationship and the effect of fishing (H_3), and ecosystem scientists concentrate on trophic interactions of adults (H_4). One purpose of this essay is to articulate this compartmentalization and to stimulate thought and effort to work across these scientific communities and to integrate across the four general hypotheses explaining variability in fisheries.

Pursuing hypotheses

Through examination of the work of Hjort, the subsequent 100 years of fisheries oceanography research, and the four general

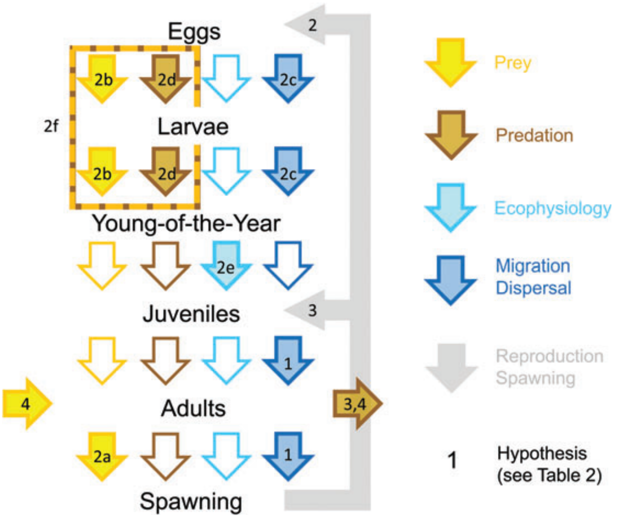

Figure 2. A schematic showing the different life stages of the typical marine fishery species and the five general processes that affect abundance and distribution: (i) prey/feeding, (ii) predation, (iii) movement/dispersal, (iv) ecophysiology, and (v) reproduction/spawning. Potentially, any process during any life stage could contribute to variability in the abundance and distribution of fishery populations. The hypotheses discussed here are indicated by solid arrows at relevant life stage and process: (H_1) migration, (H_2) year-class success, (H_{2a}) parental condition, (H_{2b}) prey environment, (H_{2c}) dispersal, (H_{2d}) predation, (H_{2e}) ecophysiology, (H_{2f}) growth-mortality, (H_3) fishing and stock–recruitment, and (H_4) adult trophic interactions. The numeric notation used throughout the text and the hypothesis are briefly described in Table 2. Unfilled arrows are life stage and process combinations that are not included here. All of these life stages and processes likely act to affect abundance and distribution of fishery species; however, the rank importance of each varies over species, populations, space, and time. There is also a large degree of interaction among processes requiring a collaborative, interdisciplinary, synthetic, multi-model approach.

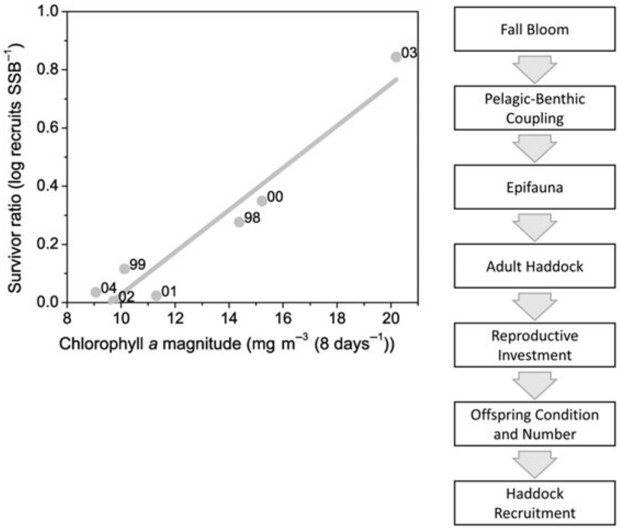

Figure 3. The relationship between the magnitude of autumn bloom and the survivor ratio (recruits per spawner) for Georges Bank haddock. The hypothesized mechanism leading to the correlation is a large autumn bloom improves the feeding conditions for adult haddock and results in a greater quality and quantity of offspring and ultimately greater year-class success and higher recruitment (modified from Friedland *et al.*, 2008). The mechanistic steps in the hypothesis from autumn bloom to recruitment are indicated by the boxes on the right side.

hypotheses presented above, five regulating processes can be identified: (i) prey, (ii) predation, (iii) movement, (iv) ecophysiology, and (v) reproduction. Reproduction is the start of the life cycle and involves a great deal of complexity (see Cole, 2010). Most marine organisms have complex life histories, with different ontogenetic stages occupying different habitats from spawning to maturity (Figure 2), and the remaining four regulating processes act during all life stages. There are interactions among all five processes resulting in the complex dynamics of fishery abundance and distribution. The ideas of prey, predation, movement, and reproduction are introduced above. Ecophysiology is the interrelationship between the abiotic and biotic environment and an organism's physiology (Neill *et al.*, 1994).

Viewing specific hypotheses and processes within the set of possible hypotheses and processes highlights the limited nature of much of our work and illuminates new areas for research (Figure 2). To achieve the goal of improving fisheries assessment and management, multiple hypotheses must be examined in more detail and incorporated into assessment models. In addition, the hypotheses not considered in an application of fisheries oceanography must at least be acknowledged. Here I discuss four hypotheses with examples from the Northeast US Shelf Large Marine Ecosystem. Two of these hypotheses were dealt with by Hjort [parental condition hypothesis (H_{2a}) and migration hypothesis (H_1)], but for whatever reason, are relatively understudied compared with the critical period hypothesis (H_{2b}) and the larval dispersal hypothesis (H_{2c}). The other two hypotheses were developed in the latter half of the 20th century: predation on early life stages (H_{2d}) and the ecophysiology of early life stages (H_{2e}).

The four hypotheses discussed here (H_{2a}, H_{2d}, H_1, H_{2e}) imply different dynamics than the traditional hypotheses (H_{2b}, H_{2c}, H_3, H_4) and their pursuit is important to understand the consequences of different regulating processes on fishery abundance and distributions. I choose to highlight these hypotheses because I think there is value in their examination: value in developing a scientific understanding of the hypotheses' regulating processes, as well as value in including these hypotheses in fishery assessment and management. Other researchers in other regions would likely choose different hypotheses. My goal is not to produce a review of fisheries oceanography nor to address all extant hypotheses related to variability in fishery populations (see Houde, 2008, for a more complete treatment). Rather I hope to stimulate thought, discussion, research, and application based on hypotheses that I feel are most deserving of pursuit. I use the term pursuit purposely. We need to actively investigate a range of hypotheses related to the dynamics of fishery populations and integrate and apply these investigations to fisheries assessment and management, no matter where the science leads us.

Parental condition hypothesis (H_{2a})

The parental condition hypothesis (H_{2a}) was considered by Hjort (1914). He examined liver weight and year-class success in Atlantic cod and found no relationship. The hypothesis was also acknowledged by Beverton and Holt (1957) in their seminal work on the stock–recruitment relationship and the importance of fishing mortality in fishery dynamics (H_3). Despite these early treatments, the parental condition hypothesis did not become a focus of researchers until the late 1980s–early 1990s (see review by Green, 2008). Both maternal and paternal effects are documented (Green and McCormick, 2005; Trippel *et al.*, 2005; Probst *et al.*, 2006). Increased parental size and weight result in larger and higher condition offspring (Hislop, 1988; Berkeley *et al.*, 2004). Increased parental condition also leads to larger and higher condition offspring (Blanchard *et al.*, 2003; Donelson *et al.*, 2008). Social conditions, such as crowding, influence offspring size and condition (McCormick, 2006). Additionally, evidence for skip spawning (failure to start egg production or resorption of eggs before spawning) has been found in many stocks and linked to poor maternal condition (Rideout *et al.*, 2000, 2005; Skjæraasen *et al.*, 2012). Finally, the environment experienced by parents can modify the phenotype of offspring, thus one life stage can affect another (Salinas and Munch, 2012).

Parental age, size, condition, and environment affect offspring size, growth, condition, and phenotype. Couple these observations with the growth-mortality hypothesis (H_{2f}, Anderson, 1988) and the hypothesis that parental condition influences year-class success is complete. The growth-mortality hypothesis (H_{2f}) holds that larger and faster growing larvae have a higher probability of survival and implicitly combines the prey environment hypothesis (H_{2b}) and the predation hypothesis (H_{2d}) (Meekan and Fortier, 1996; Hare and Cowen, 1997; Takasuka *et al.*, 2003). By inference, higher parental condition is linked to larger size, higher growth, and increased survival of early life stages, which leads to higher year-class success (e.g. Vigliola and Meekan 2002). Higher larval growth and condition, however, are not a function of the prey environment (H_{2b}), but due to the parental contribution to offspring (H_{2a}).

The ideas and concepts of the parental condition hypothesis are central to recent work on the recruitment dynamics of Georges Bank haddock. Friedland *et al.* (2008) described a significant correlation between the magnitude of autumn bloom and haddock recruitment. Haddock primarily spawn in spring, so autumn bloom is timed with the adults preparing for spawning. A number of other variables were examined (e.g. spring zooplankton, spring advection) and the correlations with recruitment were minimal providing little support for the hypotheses that prey (H_{2b}) and dispersal (H_{2c}) influence haddock recruitment. Friedland *et al.* (2008) proposed that a large autumn bloom results in increased export of material to the bottom, which improves feeding conditions for adult haddock (Figure 3). Increased parental condition results in higher quantity and quality of offspring, which leads to increased year-class success. Previous studies on haddock found parental effects on offspring size and survival (Trippel and Neil, 2004) and significant correlations between recruitment and indices of adult growth and condition (Marshall and Frank, 1999), providing ancillary support for the hypothesis of Friedland *et al.* (2008).

The parental condition hypothesis must be further evaluated. In the context of Friedland *et al.* (2008), there are a number of mechanistic links that must be studied: the conditions that lead to improved parental condition; the physiology of investment into reproduction vs. growth vs. activity; the export of energy from plankton blooms to the benthos; and ultimately, the relationship between parental condition and year-class success. The growth-mortality hypothesis provides a mechanism linking offspring condition to increased larval survival, and this hypothesis must also be tested to evaluate the mechanisms by which larger, higher condition, and faster growing early life stages result in higher recruitment. Many of these scientific questions are outside of traditional recruitment fisheries oceanography as defined over the past 30 years (Kendall and Ducker, 1998), but are directly relevant to understanding the mechanisms that affect fisheries abundance relative to the parental condition hypothesis.

The parental condition hypothesis also needs to be linked with fishery population dynamic models. This hypothesis indicates that the paradigm of a spawning-stock biomass–recruitment relationship is flawed (*sensu* Rothschild and Fogarty, 1989); the emphasis should be on the quantity and quality of offspring produced not on the combined weight of the spawning population. Major steps in this direction have been taken. Marshall *et al.* (1999) showed that spawning-stock biomass is not necessarily a robust measure of reproductive output (see also Marshall *et al.*, 2003). Further, the hypothesis implies links between reproduction, growth (prey processes), and survival (predation processes).

Parental factors have been included in population models demonstrating that the hypothesis can be incorporated into stock assessments and management advice (Óskarsson and Taggart, 2010; Shelton *et al.*, 2012). Murawski *et al.* (2001) included parental effects in a stock assessment model for Atlantic cod, specifically linking early life stage survival to the age of spawners. Their results indicate that models not including parental effects may overestimate the resiliency of a population to fishing. Another potential approach is to include the environmental effects influencing parental condition in an environmentally explicit stock–recruitment relationship (see Iles and Beverton, 1998; Köster *et al.*, 2003b). The implications of the two different approaches (modify spawning-stock biomass or model recruitment with additional terms) need to be evaluated, but the parental condition hypothesis can be used in fisheries assessment and management if the necessary information is gathered (specific mechanism, links to models).

Predation on early life stages (H_{2d})

Predation has a clear influence on population abundance but was not considered by Hjort (1914, 1926). Fishing, which is human predation, is the dominant source of mortality for many exploited species and directly affects abundance (Myers *et al.*, 1997; Christensen *et al.*, 2003). Many traditional stock assessment models (H_3) assume a constant natural mortality rate, which largely represents non-human predation mortality on post-recruitment stages. The abundance estimates resulting from these models, however, are sensitive to the magnitude and variability of natural mortality (Jiao *et al.*, 2012). Multispecies (Curti *et al.*, 2013) and foodweb models (Overholtz and Link, 2009) also include predation (or consumption) as a dominant regulating process. Traditional stock assessment methods, multispecies models, and foodweb models hypothesize the importance of predation on post-recruitment stages (H_3, H_4), yet Hjort (1914, 1926) hypothesized that fluctuations in fishery abundance were largely determined during prerecruitment stages (H_2). The difference between these hypotheses (adult predation vs. year-class success) is rarely considered.

Interest in predation during prerecruit stages increased in the late 1980s (H_{2d}, Bailey and Houde, 1989; Verity and Smetacek, 1996; Bailey and Duffy-Anderson, 2010). Studies indicate that predation on early juveniles may be a major driver of abundance in temperate and coral reef ecosystems (Carr and Hixon, 1995; Tupper and Boutilier, 1997). Takasuka *et al.* (2003), in an elegant study, showed that predation was higher on slower growing larvae, providing direct evidence for an inverse relationship between larval growth and predation (H_{2f}) and demonstrating an interaction between the processes that affect growth (prey) and those that affect survival (predation).

Two recent lines of investigation further emphasize the role of predation on early life stages in determining year-class success and ultimately adult abundance. First, predation on groundfish larvae by pelagic fish adults has been proposed as a mechanism for low groundfish recruitment and for keeping groundfish populations at low levels even after decreases in fishing effort (e.g. Köster and Möllmann, 2000). Modelling shows that predation on groundfish larvae can be important to population dynamics (Collie *et al.*, 2013) and field studies have found spatial and temporal overlap between groundfish larvae and pelagic fish adults (Garrison *et al.*, 2000, 2002). Second, predation on benthic eggs by groundfish predators has been hypothesized to regulate Atlantic herring abundance on the northeast US continental shelf (Richardson *et al.*, 2011). A model incorporating Atlantic herring spawning-stock biomass and egg predation by haddock predicts the abundance of larvae on Georges Bank over the past four decades (Figure 4). This model is supported by feeding studies that found haddock with large proportions of fish eggs in their stomachs (Langton and Bowman, 1981; Toresen, 1991). In the western Baltic Sea, Polte *et al.* (2014) found a significant correlation between Atlantic herring yolk-sac larvae and interannual variability in year-class success. They concluded that egg mortalities are a likely cause for recruitment variability. These predation hypotheses remain controversial in part because time-series analyses have not identified a link between groundfish and pelagic fish dynamics (Liu *et al.*, 2012; Swain and Mohn, 2012).

The predation hypothesis (H_{2d}) needs to be investigated further. The ability to model larval feeding is quite advanced (e.g. Fiksen and MacKenzie, 2002), yet the ability to model predation on eggs and larvae is relatively rudimentary (but see Fuiman *et al.*, 2006). Most biophysical numerical models do not explicitly include predation. Predation is often implicitly assumed to be constant over time and space (e.g. Cowen *et al.*, 2000) or based on size- or growth-specific mortality functions [e.g. the growth-mortality hypothesis (H_{2f}), Hermann *et al.*, 2001; Kristiansen *et al.*, 2011]. Recent biophysical modelling studies demonstrate the potential importance of including time and space varying predation (e.g. North *et al.*, 2009; Ji *et al.*, 2012). Going forward, predators in planktonic systems must be identified and enumerated. Detailed diet studies (Llopiz *et al.*, 2010; Llopiz, 2013) and genetic techniques (Cleary *et al.*, 2012; Fox *et al.*, 2012) provide a path forward and reveal new insights into predator–prey dynamics. Similarly, optical and acoustic techniques provide a means to study the distribution of plankton predators and their overlap with early life stages (Hallfredsson and Pedersen, 2009; Greer *et al.*, 2013). Predation rates and functional forms of prey consumed relative to prey density must also be measured and parameterized for use in models (Purcell and Grover, 1990; Gentleman and Neuheimer, 2008). Finally, early life stage predation needs to be incorporated into fisheries assessments models. The work of Collie *et al.* (2013) and Richardson *et al.* (2011) indicates that early life stage predation (H_{2d}) can result in multiple equilibrium points in fishery populations, which create very different population dynamics than implied by the standard assessment models (H_3; see also Steele and Henderson, 1984; Bakun, 2006).

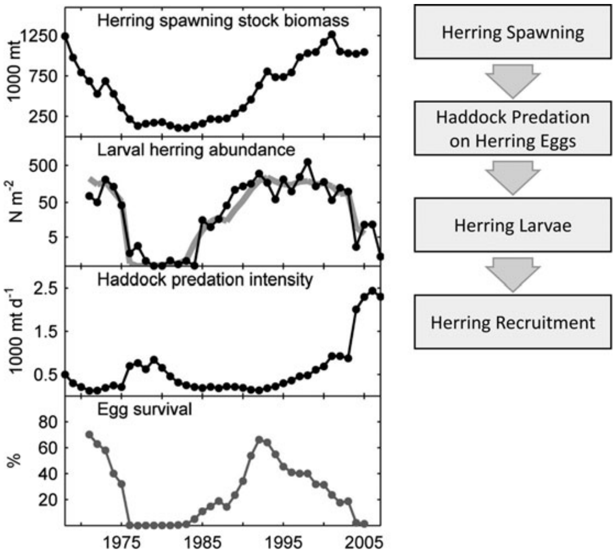

Figure 4. Time-series of Georges Bank/Gulf of Maine Atlantic herring spawning-stock biomass, larval index, haddock predation intensity, and estimated egg survival. The observed larval index (black line) was compared with a modelled larval index (grey line). The model assumes egg production is proportionate to spawning-stock biomass and then applies haddock predation to the egg biomass where haddock predation is estimated by numbers-at-age and consumption-at-age derived from survey and field studies. Through time, variable haddock predation results in variable Atlantic herring egg survival and the number of larvae estimated by the model closely matches the number of larvae observed in surveys (modified from Richardson *et al.*, 2011). The mechanistic steps in the hypothesis from Atlantic herring spawning to recruitment are indicated by the boxes on the right side.

Migration hypothesis (H_1)

Despite Hjort's (1914) rejection of the migration hypothesis (H_1), there is growing evidence that changes in distribution and migration patterns affect local abundance and potentially overall abundance. Many studies have demonstrated changes in species distribution related to changing environmental conditions (Perry *et al.*, 2005; Mueter and Litzow, 2008; Nye *et al.*, 2009; Pinsky *et al.*, 2013). Changes in the distribution of fisheries have also been observed (Overholtz *et al.*, 2011; Pinsky and Fogarty, 2012). The conceptual model is that as the environment changes, the distribution of the niche changes and, as a result, species distribution changes (see Guisan and Thriller, 2005). The niche is defined as a multidimensional space within which an organism can survive and reproduce (Hutchinson, 1957); the dimensions are components of the organism's environment including biological, physical, chemical, and geological factors (Andrewartha and Birch, 1954). The basic niche is the full range of environmental conditions within which a species can survive and reproduce; the realized niche is the subset of the fundamental niche used by a species as a result of ecological interactions (e.g. competition, predation, feeding). These ideas have been used to develop niche-models of marine species and forecast changes in distribution in response to climate change (Lehodey *et al.*, 2003; Chueng *et al.*, 2009; Hare *et al.*, 2012).

Atlantic mackerel in the North Atlantic provide an excellent example of changes in regional abundance owing to changes in distribution over time. In the Northwest Atlantic, Atlantic mackerel overwinter off the northeast US shelf and during summer, contingents spread to the Gulf of Maine, Gulf of St Lawrence, and near Newfoundland. Overholtz *et al.* (2011) documented a northward and landward shift of overwintering groups associated with warming shelf waters. This resulted in a decrease in abundance in a recreational fishery, which took place in historical overwintering grounds. Radlinski *et al.* (2013) emphasized changes in distribution along the northeast US shelf were partially explained by environmental changes, but fish size was also an important factor. In the Northeast Atlantic, changes in Atlantic mackerel distribution are more extreme. Astthorsson *et al.* (2012) reported that Atlantic mackerel were intermittently found around Iceland from 1895 to 1996. Starting in 2007, large numbers of Atlantic mackerel were found around Iceland and a commercial fishery developed. Astthorsson *et al.* (2012) linked the increase in Atlantic mackerel to warming which started in the 1990s but also suggested other factors may be involved including changes in population size and the age/size structure of the population. Jansen and Gislason (2013) proposed that strong year classes of mackerel stray into other areas for spawning as adults and thus, movement, distribution, age-structure, and productivity are related.

The mechanisms and consequences of changes in distribution must be pursued to more fully understand fluctuations in fishery populations. In the instances of species shifts in response to environmental change, not all species shift similarly. For example, on the northeast US shelf, 17 stocks shifted poleward, 4 stocks shifted equatorward, and 15 stocks showed no change over a 40+ year record (Nye *et al.*, 2009). Understanding the differences among species will help elucidate the mechanisms that shape species distributions and movements. Species distributions also change as a result of changes in age-structure, size-structure, and condition; thus, changes in growth (prey processes) and survival (predation processes) are linked to changes in distribution (Bailey *et al.*, 1982; Slotte, 1999; Radlinski *et al.*, 2013). The energetics of migration in the context of other energetic demands (e.g. reproduction, growth, basal metabolism) also needs to be further elucidated (reproduction and ecophysiology processes) (Nisbet *et al.*, 2012). Finally, the distribution of and movement among different habitats (e.g. spawning, overwintering, feeding) needs to be examined (e.g. Anderson *et al.*, 2013). Similar to the predation hypothesis (H_{2d}) and the parental condition hypothesis (H_{2a}), the movement hypothesis combines multiple processes related to variability in the abundance of fishery species.

A major question for fisheries assessment and management is whether individuals are changing their distribution or the productivity of individuals in different locations is changing. The former means changing availability to fisheries and changing stock boundaries (Link *et al.*, 2011); the latter means changing population dynamics and management reference points (Quinn and Collie, 2005). As an example of shifts in distribution, changes in bluefin tuna migration pathways have been linked to environmental, trophic, and fishing pressures and have resulted in changes in local abundance (Ravier and Fromentin, 2004; Fromentin, 2009). As an example of changes in productivity, shifts in Atlantic surfclam distributions resulted from mortality in shallower waters from thermal stress (Weinberg, 2005). Similarly, anchovy have expanded in the North Sea owing to increased productivity of existing remnant populations, which resulted from an expansion of thermal habitat (Petitgas *et al.*, 2012). Changes in distributions can result in social and economic impacts; examples include Atlantic mackerel off Iceland (Astthorsson *et al.*, 2012) and fishery species moving into the Gulf of Maine (Mills *et al.*, 2013). Examining the migration hypothesis and understanding species distributions in a variable and changing environment is critical to accurately assess and successfully manage fisheries.

Ecophysiology (H_{2e})

Ecophysiology is the interrelationship between the environment and an organism's physiology (Fry, 1971; Neill *et al.*, 1994). Using temperature as an example, a range of biological processes are related to temperature either directly or indirectly (Brett, 1979; Pörtner *et al.*, 2001; Pörtner, 2002; Brown *et al.*, 2004). All organisms have thermal limits above and below which death is rapid. Within these limits, temperature controls a number of rate processes, including gene expression, enzyme kinetics, metabolism, activity, consumption, and growth. Organisms also respond behaviourally to temperature through migration, foraging, and resting. Temperature is also related to individual survival and fitness, as well as population growth rate (Brown *et al.*, 2004; Kingsolver, 2009). Temperature is a component of the basic niche, which is important in shaping species distribution and abundance (Hutchinson, 1957; Kerr and Werner, 1980; Magnuson and DeStasio, 1997). Similar biological processes are related to other environmental factors, including dissolved oxygen (Craig and Crowder, 2005; Prince and Goodyear, 2006), salinity (Attrill and Rundle, 2002; Lowe *et al.*, 2012), and contaminants (Matthiessen *et al.*, 2002; Brooks *et al.*, 2012). This view of ecophysiology is closely related to the metabolic theory of ecology (Brown *et al.*, 2004).

One example of temperature affecting abundance and distribution is overwinter mortality in temperate ecosystems. Overwinter mortality is caused by the physiological response to temperature combined with the relative scarcity of food and potential susceptibility to predation (Hurst, 2007). Along the east coast of the United States, overwinter mortality affects the distribution and abundance a number of fishery species including pink shrimp (Hettler, 1992), reef fish (McBride and Able, 1998; Parker and Dixon, 1998), striped bass (Hurst and Conover, 1998), Atlantic croaker (Hare and Able, 2007), blue crab (Bauer and Miller, 2010), red drum (Anderson and Scharf, 2014), and grey snapper (Wuenschel *et al.*, 2012). For Atlantic croaker, laboratory studies found decreased juvenile survival below 3°C (Lankford and Targett, 2001a, b). Field studies in spring confirm that juvenile abundance is related to winter water temperature (Hare and Able, 2007). As a result, recruitment to the adult population is also related to winter temperature and a population model including an empirical temperature-dependent recruitment function replicated the past patterns in Atlantic croaker abundance (Figure 5, Hare *et al.*, 2010). Further, Hare *et al.* (2010) developed a one-dimensional distribution model using population size and winter temperature as independent variables. The example of overwinter mortality indicates that the environment can limit fishery population abundance and distribution through ecophysiological processes.

Ecophysiology has been part of fisheries oceanography since Hjort (1914, 1926), but the emphasis is on the physiological interaction between the environment and the organism (ecophysiology), rather than the organism obtaining resources from the environment (e.g. starvation and the critical period hypothesis). Since these ideas are not new, there have been many calls for increasing our understanding of ecophysiology (Neill *et al.*, 1994; Helmuth *et al.*, 2006; Helmuth, 2009; Pörtner, 2010). That said, there are several research areas that would lead to better integration between ecophysiology and the other processes of importance to fishery abundance and distribution. First, the allocation of energy among basal metabolism, growth, reproduction, daily activity, and seasonal activity needs to be understood and quantified. A similar research need was identified for the parental condition hypothesis and the migration hypothesis. Second, the effect of temperature and other environmental variables on physiology and energy allocation needs to be examined. Third, the combined role of prey, predators, physical environment, and physiology needs to be developed in terms of

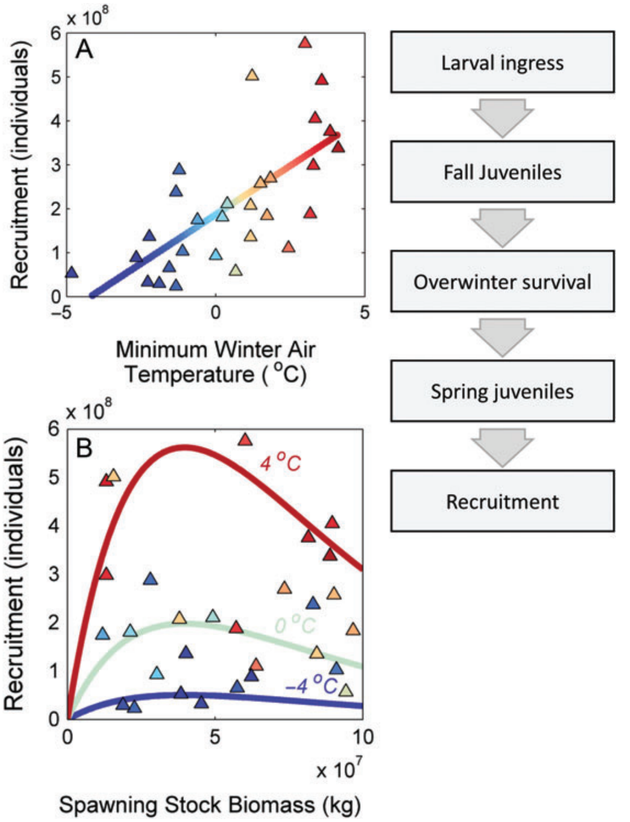

Figure 5. The relationship between winter temperature and recruitment of Atlantic croaker. The correlation supports the hypothesis that overwinter survival determines year-class success in Atlantic croaker. A recruitment-spawning-stock biomass function including winter temperature fits observed recruitment much better than a function without the environmental term. The colour of the symbols represents winter temperature. The lines in the recruitment-spawning-stock biomass panel shows estimated recruitment at a mean winter temperatures of −4°C, 0°C, and 4°C (modified from Hare *et al.*, 2010). The mechanistic steps in the hypothesis from larval ingress into juvenile habitats to recruitment are indicated by the boxes on the right side.

individual survival and population growth rates. This information could be used to parameterized process-oriented models of distribution, growth, survival, and recruitment (e.g. Okunishi *et al.*, 2012) in contrast to populations models using empirical environment–biological response functions (e.g. temperature-recruitment, Hare *et al.*, 2010).

Conclusions: the legacy of Johan Hjort

The goal of fisheries oceanography is to understand the oceanographic and ecological processes that affect fishery abundance, distribution, and availability and then apply this understanding to improve fisheries assessment and management. In this essay, I considered fisheries oceanography from the perspective of fishery abundance and distribution. The examination of the four hypotheses above (H_{2a}, H_{2d}, H_1, H_{2e}) indicates that abundance and distribution are related. This idea is well captured by the Basin Hypothesis (MacCall, 1990). Taking some liberties with this hypothesis, distribution is linked to the abundance of the population and dimensions of the niche (or the distribution of essential fish habitat). This concept was also recognized by Hjort who discussed the migration hypothesis in terms of "sensitivities" of species responding to changes in the environment. The niche concept is defined above; essential fish habitat is defined as all the areas necessary for fish reproduction, feeding, growth, and survival (Beck *et al.*, 2001; Manderson *et al.*, 2002). Thus, essential fish habitat represents a subset of the basic niche that is similar to the realized niche. The distribution of the niche and essential fish habitat is related to distribution and abundance of fishery species (MacCall, 1990; Bartolino *et al.*, 2011) and there is strong evidence that overall population abundance is controlled by the area available, or in other words the multidimensional area of the niche and the amount of habitat (Sinclair, 1988; MacKenzie *et al.*, 2003).

From the review of the four hypothesis above (H_{2a}, H_{2d}, H_1, and H_{2e}), it is also clear that the regulating processes of prey, predators, movement, ecophysiology, and reproduction vary through time and space. This implies that the niche and essential fish habitat concepts must be viewed as dynamic: varying and changing as a result of the interaction among the regulating processes (Figure 2, MacKenzie *et al.*, 2007; Cheung *et al.*, 2011). Further, these regulating processes act in most life stages and can act in one life stage and have consequences for subsequent life stages. In all likelihood, in different portions of a species range, the relative contribution of different processes at different life stages varies (e.g. Neill *et al.*, 1994; Myers, 1998). Similarly, as climate and fishing pressure vary and change, the temporal contribution of the different processes acting at different life stages likely changes (e.g. Petitgas *et al.*, 2012). This results in a complex pattern of fishery abundance and distribution that varies and changes owing to variability and changes in the regulating processes and subsequently the dimensions of the niche and the quality and quantity of habitat (Figure 6). To improve forecasts and predictions of abundance and distribution, we need to understand the action and interaction of the five regulating processes. Further, we need to incorporate these processes and their related hypotheses in fisheries assessment and management. We can simplify by focusing on one or a subset of hypotheses and processes, but we must be careful to recognize the limitations of our simplifications, and improve or change our approach when science dictates (Ianelli *et al.*, 2011; Link *et al.*, 2011).

Much of the focus here has been on populations and species as they relate to single-species assessment and management. There has been a broad call for Ecosystem-Based Fisheries Management (EPAP, 1999; Pikitch *et al.*, 2004) and a call for a transition from fisheries oceanography to ecosystem oceanography (Cury *et al.*, 2008). The ideas discussed here are relevant to broader ecosystem approaches. The "basin" described above (Figure 6) is for a single species or population but includes interactions with components of the ecosystem and the environment. A multispecies approach can be envisioned as multiple interacting "basins", one for each population or species. An ecosystem-approach can be envisioned as interacting "basins" for functional groups or communities. An important issue regarding multispecies, functional group, or community level aggregation is the ability to combine populations/species and life stages and treat them similarly from an ecological, fishery, and socio-economic perspective. This combination is similar to the difference between a stock (a management unit) and a population (an ecological unit) (see Secor, 2013), but at higher-levels of organization. Understanding the implications of such aggregation, investigating different approaches to aggregation, and parameterizing aggregation should be a focus of future fisheries oceanography research and an integral part of the development of Ecosystem-Based Fisheries Management.

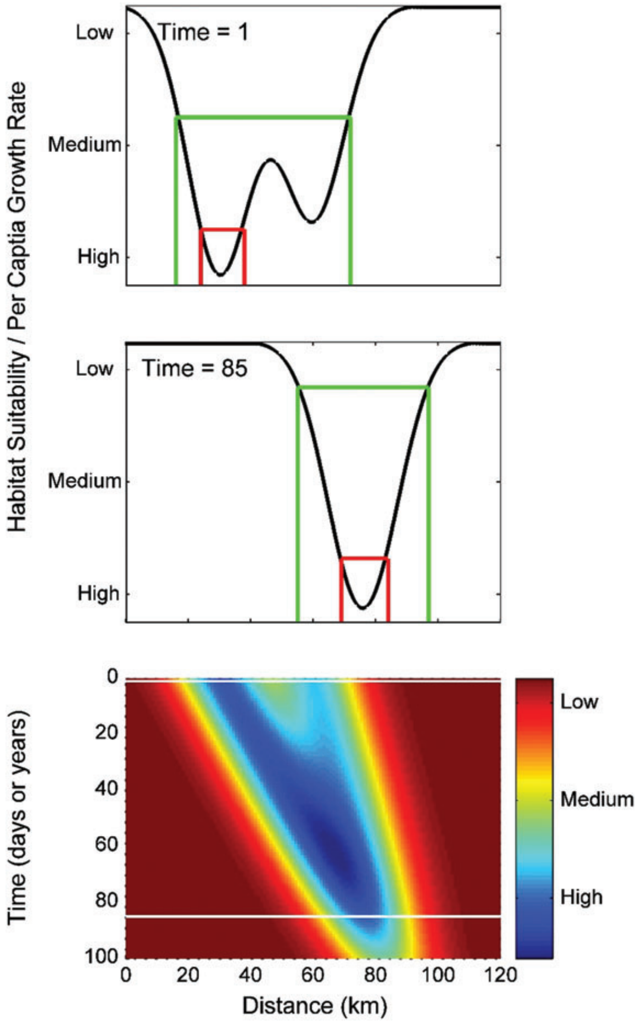

Figure 6. A schematic of the Basin Hypothesis (MacCall, 1990) showing changes in the shape and the distribution of the "basin" through the life history or for one life stage through time. The red line shows the distribution at low population abundance. The green line shows the distribution at high population abundance. The "basin" represents habitat quality or population growth rate and is analogous to the niche of the species. The "basin" includes the effect of all the processes affecting abundance and distribution (prey, predation, movement, ecophysiology, and reproduction). The shape of the "basin" changes through time which will affect the abundance and distribution of fishery species. This schematic is further complicated by the complex life history of most marine organisms; each life stage potentially having its own basin.

Another focus moving forward needs to be the development of models that integrate understanding and improve assessments, be they single species, multispecies, or ecosystem assessments. These models need to span a range of complexity and address a range of hypotheses (Figure 2). Most of the models currently used in fishery stock assessment are based on fishing mortality and a spawning-stock biomass–recruitment relationship (H_3), but recently other hypotheses and processes have been integrated into the stock assessment framework (e.g. Murawski *et al.*, 2001; Quinn and Collie, 2005; Ianelli *et al.*, 2011). Most oceanographic and climate models include bottom-up effects on early life stages (H_{2b}) or environmentally driven niche-models (H_{2e}). Much of the ecological and ecosystem modelling includes foodweb dynamics (H_4) but excludes early life stages. The structure of a model will limit the potential findings (aka structural uncertainty; see McAllister and Kirchner, 2002; Essington and Plagányi, 2014). For example, the structure of nutrient–phytoplankton–zooplankton models determines whether bottom-up or top-down processes are found to be important (Sailley *et al.*, 2013). Given the variety of hypotheses for the determinants of abundance and distribution of fishery species, the amount of structural uncertainty in our present assessments and management is higher than we typically recognize. This uncertainty needs to at least be recognized and then future efforts should work to decrease this uncertainty.

One could argue that the research questions and path forward identified here represents "more of the same": more reductionist science and building more complicated models. This is a valid criticism, but I would counter that the emphasis moving forward needs to be integrating among hypotheses and processes incorporated into models. Yes, we need to continue our investigation of individual hypotheses (reductionist science), but at the same time, we need to broaden our view and integrate among hypotheses and processes. Additionally, we need to pursue hypotheses and not automatically keep working within the traditional hypotheses. Thus, I recommend we focus on Hjort's approach, as well as the hypotheses attributed to him. Hjort proposed and pursued multiple hypotheses using interdisciplinary science. He moved away from the migration hypothesis (H_1) based on evidence at the time and was willing to propose and investigate different hypotheses. Perhaps he knew of Chamberlin's (1890) work on "multiple working hypotheses", an idea which is again gaining momentum (Burnham and Anderson, 2002). Following Hjort, a hundred years of reductionist science investigating single hypotheses and processes has created isolated paradigms. We need to follow Hjort's approach and combine and integrate our understanding of the various processes that affect fishery abundance and distribution. We then need to apply to this science to improve fishery assessment and management.

Acknowledgements

This essay benefited for many people over the years who have shaped my thinking on fisheries oceanography. In particular, Bob Cowen, Ken Able, Jeremy Collie, Mike Fahay, Mike Fogarty, Kevin Friedland, Jeff Govoni, Anne Hollowed, John Manderson, Dave Richardson, Cisco Werner, and Mark Wuenschel. Also the participants of the NOAA NMFS FATE programme (Fisheries and the Environment) provide stimulating science and ideas helping to move fisheries oceanography forward; in particular, I would like to acknowledge the FATE programme managers Kenric Osgood and Michael Ford. I also thank three anonymous reviewers, David Richardson, John Manderson, Rich Bell, and Howard Browman for their constructive and thought-provoking comments on earlier drafts; this work greatly benefited from their input. Acknowledgement of the above individuals does not imply their endorsement of this work; I have sole responsibility for this contribution. The views expressed herein are mine and do not necessarily reflect the views of NOAA or any of its subagencies.

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Handling editor: Howard Browman

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2014), 71(8), 2357–2369. doi:10.1093/icesjms/fsu116

Contribution to the Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe'

Quo Vadimus

Marine ecosystem acoustics (MEA): quantifying processes in the sea at the spatio-temporal scales on which they occur

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Godø, O. R., Handegard, N. O., Browman, H. I., Macaulay, G. J., Kaartvedt, S., Giske, J., Ona, E., Huse, G., and Johnsen, E. Marine ecosystem acoustics (MEA): quantifying processes in the sea at the spatio-temporal scales on which they occur. – ICES Journal of Marine Science, 71: 2357–2369.

Received 27 March 2014; revised 29 May 2014; accepted 9 June 2014; advance access publication 22 July 2014.

Sustainable management of fisheries resources requires quantitative knowledge and understanding of species distribution, abundance, and productivity-determining processes. Conventional sampling by physical capture is inconsistent with the spatial and temporal scales on which many of these processes occur. In contrast, acoustic observations can be obtained on spatial scales from centimetres to ocean basins, and temporal scales from seconds to seasons. The concept of marine ecosystem acoustics (MEA) is founded on the basic capability of acoustics to detect, classify, and quantify organisms and biological and physical heterogeneities in the water column. Acoustics observations integrate operational technologies, platforms, and models and can generate information by taxon at the relevant scales. The gaps between single-species assessment and ecosystem-based management, as well as between fisheries oceanography and ecology, are thereby bridged. The MEA concept combines state-of-the-art acoustic technology with advanced operational capabilities and tailored modelling integrated into a flexible tool for ecosystem research and monitoring. Case studies are presented to illustrate application of the MEA concept in quantification of biophysical coupling, patchiness of organisms, predator–prey interactions, and fish stock recruitment processes. Widespread implementation of MEA will have a large impact on marine monitoring and assessment practices and it is to be hoped that they also promote and facilitate interaction among disciplines within the marine sciences.

Keywords: acoustics, assessment, ecology, ecosystem-based fisheries management, ecosystem models, physical–biological coupling, recruitment processes, spatio-temporal scaling.

Introduction

After observing the connections between sea surface temperatures along the coast of Western Norway, and subsequent biological changes in the Barents Sea, Helland-Hansen and Nansen stated "*We think that these discoveries give us the right to hope that by continued investigations it will be possible to predict the character of climate, fisheries, and harvests, months or even years in advance*" (Helland-Hansen and Nansen, 1909). This represents an early conceptualization of what we now refer to as fisheries oceanography.

Since Johan Hjort developed his recruitment hypothesis (Hjort, 1914), fisheries scientists have struggled to understand the drivers of variability in the population dynamics of commercially important fish and shellfish populations. Fisheries oceanography has sought to understand the influence of the physical environment on these processes. Fisheries scientists, utilizing data from commercial fishing, developed survey tools and population models to assess the status of harvested stocks and to set future (sustainable) catch levels. The inability of marine ecologists to collect data on the spatial and temporal scales that are possible in terrestrial and intertidal environments has limited the development of a more process-oriented fisheries oceanography that incorporates mainstream ecological theory (see Stergiou and Browman, 2005).

Ecosystem-based fisheries management (EBM) has been widely adopted by stewardship agencies in an attempt to more effectively manage the direct and collateral impacts that fishing and other human activities impose on the oceans (Bianchi and Skjoldal, 2008; McLeod and Leslie, 2009; Link, 2010; Kruse *et al.*, 2012). EBM also represents an (as yet unrealized) opportunity to incorporate more ecological theory into fisheries oceanography.

Fisheries oceanography has typically been divided into the traditional trophic control paradigms of bottom-up and top-down forcing. However, it has increasingly been acknowledged that trophic forcing is dynamic and may shift considerably in time and space (e.g. Cury *et al.*, 2000; Frank *et al.*, 2007). A natural extension of Hjort's fisheries oceanography paradigm is, therefore, the move towards an *ecosystem oceanography* (*sensu* Cury *et al.*, 2008): the study of interactions among ecosystem components and drivers at the level of the population, the foodweb, and the ecosystem. Ecosystem oceanography aims to understand each organizational level by confronting model results with the empirical reality expressed in the data. We must, therefore, build models that incorporate the key ecological processes and carry out subsea observations on spatial and temporal scales that can inform these models. Unfortunately, this has proven impossible to achieve with classical sampling methods and equipment.

Operationalizing *ecosystem oceanography* requires models linked to synoptic observations and sampling of the ocean's biological and physical characteristics (see, e.g. Handegard *et al.*, 2012b; Demer *et al.*, 2009). Hans Lassen, a former Head of the ICES Advisory Programme, states that the data demanded by the ecosystem approach cannot possibly be met because of the costs involved with the use of present technology. He foresees new technologies taking over: "*Or would a technological breakthrough in LIDAR or hydroacoustics (e.g. multifrequency techniques) be the way forward?…* ***I believe that these and many other technological changes will be seen in the not too distant future*** "(ICES Inside Out, 2010, No. 4, p. 2). In this context, Koslow (2009), Trenkel *et al.* (2011), and Handegard *et al.* (2012b) explore the possibility of simultaneously collecting physical and acoustic information about the identity and distribution of organisms to integrate the two and assess biophysical coupling at previously inaccessible spatio-temporal scales (e.g. Godø *et al.*, 2012; Kaartvedt *et al.*, 2012).

The reintroduction of ecology into fisheries oceanography through the EBM makes this a timely effort. On a general level, ecology can be defined as, "the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance" (Krebs, 1972; Begon *et al.*, 1986). This definition focuses on the organism and, once the organism is detected and classified, its abundance can be determined by investigating its spatial and temporal distribution. In the sea, acquiring such knowledge highlights three crucial observational challenges: *detection, identification, and enumeration*. Understanding variation in abundance and distribution requires interpretation of inter- and intra- specific interactions, as well as biophysical coupling and physical forcing on the spatial and temporal scales at which these interactions occur. This leads to the fourth challenge, *coverage*, i.e. our ability to observe ecosystem components, and their interactions. To date, this has been impossible for operational reasons. Therefore, efficient sampling strategies combined with mathematical and statistical modelling have gradually become indispensible tools with the ability to combine observations of physics, individuals, and interactions at appropriate scales of time and space.

Historically, fisheries oceanography began as a natural science focused on making basic exploratory observations. Only recently has it focused on assessing patterns and processes. However, this modern focus has highlighted the limits imposed by traditional capture-based sampling methods. Henry Stommel first described the inefficiency of oceanographic surveys that do not take into account that patterns and dynamics must be observed at appropriate temporal and spatial scales (Stommel, 1963). His thinking has been incorporated into marine ecology and the original three-dimensional Stommel diagram, which visualizes variability in physical properties, has also been used to visualize the various scales upon which abundance varies in plankton communities (Haury *et al.*, 1978 and see Figure 1). The challenges associated with appropriate spatio-temporal sampling in relation to observing key features of the ecosystem have been thoroughly described (see overview in Vance and Doel, 2010). As stated by Herman and Platt, "the sampling grid has to be at least as fine-scaled as the scale of the process of interest" (Herman and Platt, 1980, p. 204). Several specific examples that illustrate this follow.

It is commonly assumed that the growth rate and survival of fish larvae depends primarily upon food availability (which is not the same as prey abundance) and predation (see, e.g. Pepin, 2004; Houde, 2009; Hare, 2014). However, this has not yet been properly resolved or validated in the field as traditional sampling gear aggregate predators and prey over volumes and times much larger than those at which these processes occur (see, e.g. Pepin, 2004; Houde, 2008). Global as well as local circulation models, which are used for studying the impact of climate change, operate on hundreds of meters to hundreds of kilometre grid resolutions. These are orders of magnitude larger than those required for ecosystem process studies. Currently, predictions of large-scale climate models, as well as ecosystem assessment models, depend substantially on unvalidated assumptions about the scaling of patterns and processes. Importantly, as stated by Levin (1992), "the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology" (p. 1943). The marine ecosystem acoustics (MEA) concept establishes observation systems that fill this data requirement gap.

MEA will achieve this goal by (i) building an observation system with acoustics as the main tool; (ii) combine that with enhanced deployment and operational capabilities; and (iii) tailor the output for use in modelling in an integrated platform that generates information resolved to taxon and collected at previously inaccessible spatio-temporal scales.

Thus, the MEA concept bridges the gap between single stock assessment and management, and methods for assessment, prediction, and management practice of harvested ecosystems in accordance with EBM. The data stream produced by MEA will enable representation of the population characteristics (identity, size, number, biomass, behaviour) of the main components of marine ecosystems. Following Levin (1992), a main challenge for the modelling component is "retaining essential information without getting bogged down in unnecessary detail" (p. 1944), i.e. moving from fine scales to broad scales, and *vice versa*, without losing essential information. Under EBM, the focus must be to maintain the quantification details needed to understand and assess exploited stocks without being confounded by the details of the marginal processes behind it. The MEA sensors produce a complex data stream that limit the viability of the MEA concept unless simulation models are developed that exploit the potential

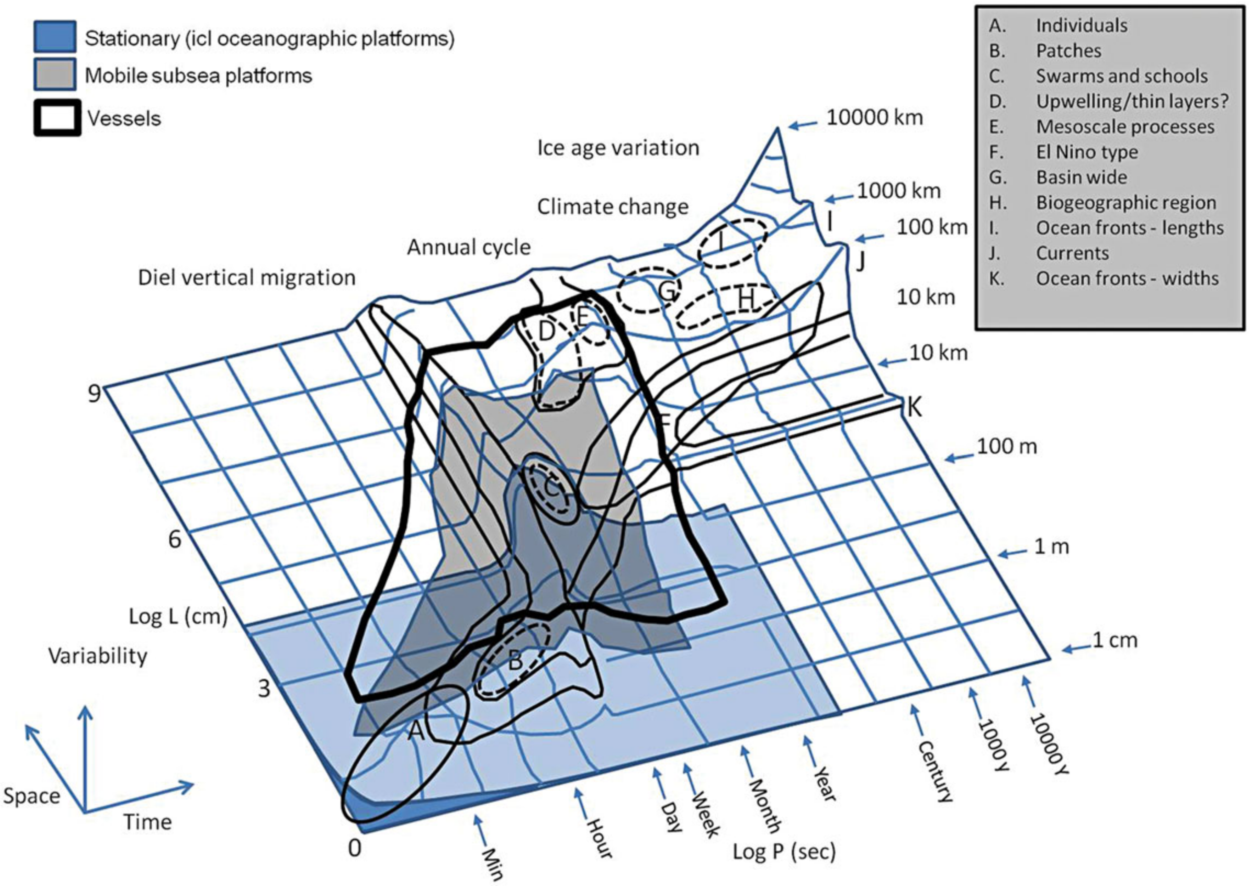


Figure 1. Modification of the Stommel diagram adopted from Haury *et al*. (1978). The surface illustrates time–space variation in plankton and higher trophic level biomass. Phenomena of importance to ecosystem understanding and assessment, and their extension in time and space are indicated on the top of the variability surface and are identified by capital letters. The diagram is extended to illustrate the use of various platforms under the MEA concept; their coverage potential, overlap and uniqueness in time and space. Stationary here includes stationary and oceanographic platforms. Vessels include vessel and vessel operated tethered platforms.

of the acoustics and operational technologies, and *vice versa* (Handegard *et al*., 2012b). Furthermore, the limited time–space coverage of ocean observations associated with the deployment of research vessels and/or moored instrument packages severely constrains our parameterization and prediction capabilities. Improved and increased application of unstructured acoustic data from ships of opportunity will, therefore, also be important. This endeavour will benefit from the ongoing development of tools and approaches to analysing very large datasets ("big data"; e.g. Schadt *et al*., 2010; Halevi and Moed, 2012; Levy *et al*., 2014; Soranno and Schimel, 2014).

In short, advances in acoustics have, in principle, made it possible to collect information on marine organisms of all sizes (fish eggs and larvae, zooplankton, and larger) by identifying and sizing them, and by observing them at previously inaccessible spatial and temporal scales. In achieving this, MEA would respond to basic challenges in ecology as well as in fisheries science and this paper aims to describe how and why this might be possible in the long term. We next describe how the opportunities offered by this sensor technology can be operationalized.

Operationalizing the MEA concept

MEA requires a balanced and efficient use of acoustic sensor technology combined with appropriate operational skills and an active and coordinated feedback loop with the development of process models. This is described in detail in the sections that follow.

Sound in the ocean is analogous to light in the atmosphere: just as the atmosphere is transparent to light, so is the ocean transparent to sound. In the ocean, sound propagates readily, while light is rapidly absorbed and otherwise diffracted by a multitude of small-scale heterogeneities of which sound, with a much longer wavelength, is relatively unaffected. This recognition has permeated research in underwater sound over the past century. It was early discovered that fish could be detected by echolocation, and the presentation of the first echograms of spawning skrei in Lofoten, by Oscar Sund in 1935 (Sund, 1935), was among the findings that stimulated the development of fisheries acoustics. By 1960, techniques for acoustic quantification of fish had been developed (Dragesund and Olsen, 1965) and these continue to be developed and refined so that it is now possible to determine the distribution and abundance of fish stocks using acoustics (e.g. Simmonds and MacLennan, 2005).

Recent advances in acoustics present new possibilities in assessment and management. Remote classification of target categories using multiple frequency scientific echosounders is a promising technique that is currently used but is still under development (Kloser *et al*., 2002; Korneliussen and Ona, 2002). The expanded observation volume of new scientific multibeam echosounders and sonars (Trenkel *et al.*, 2008; Ona *et al.*, 2009), operating at ultrasonic frequencies, makes it possible to quantify the abundance and school structure of organisms near the surface (Misund *et al.*, 2005; Ona *et al.*, 2006). Although expanding the high-frequency range using broadband technology is still in its infancy, there is the potential to enhance spatio-temporal resolution down to 1 cm and 1 s as well as increase the accuracy of species or target category separation.

Expanding bandwidth towards lower frequencies facilitates studies of organismal abundance and collective behaviour over distances of up to 100 km (Makris *et al.*, 2009). All of these improvements will generate massive amounts of new information in marine science. However, our ability to exploit these technical advances in an operational ecosystem oceanography depends on: (i) efficient post-processing and seamless flow of acoustics data from observation platforms to users, (ii) models tailored to the available data, (iii) systems for integrating acoustic data from different platforms, and (iv) researchers trained to address the vast quantity and diversity of these data.

Alternative platforms are being developed that enable *in situ* observation of plankton and fish at the resolution upon which processes occur (Godø *et al.*, 2005; Onsrud *et al.*, 2005). Flexibility in platform and sensor combinations moves observation systems for fisheries oceanography towards those used for physical oceanography (Handegard *et al.*, 2012b). Such observations are vital to the quantification and modelling of stock distribution and abundance, migration, and the critical life history events that determine recruitment.

The most advanced biophysically coupled fisheries oceanographic models have been developed using observations made at spatio-temporal scales that do not match those on which key productivity-determining processes occur (e.g. predation; starvation; fine-scale distribution; recruitment; Pepin, 2004; Houde, 2008). To make further progress, observation systems that resolve these processes, and routinely integrate the data collected into process and ecosystem models, are required.

We herein present MEA as an approach to achieve this objective. The MEA concept utilizes emerging opportunities in *acoustic sensor technologies* combined with advanced *operational capabilities*, tied together with tailored *modelling* designed to address basic scientific questions in marine ecology and fisheries oceanography as well as fill the knowledge and data gaps required to operationalize EBM.

Acoustics sensor technology

Spatial resolution is obtained by moving the acoustic sensor, by using multiple spatially distributed sensors, or by tracking the organisms within the acoustic beam. Under the MEA concept, resolution will be expanded to permit identification of individuals at centimetre scales all the way to processes taking place on scales of tens of kilometres. The tools and techniques that are currently available to accomplish this are briefly described below.

Higher frequencies and associated shorter pulses and wavelengths resolve the sampling volume better than lower frequencies. Sonars in the low-frequency band resolve schools of fish at scales of up to 100 km (Makris *et al.*, 2006, 2009), while echosounders with frequencies ∼100 s of kHz yield centimetre-scale resolutions. Broadband technology that uses pulse compression techniques can further enhance resolution to millimetre scales in the high-frequency band (see, e.g. Stanton, 2009). Split-beam echosounders, discrete frequencies as well as broadband, allow target tracking of individuals (Brede *et al.*, 1990; Handegard *et al.*, 2005). High-frequency, broadband systems with split-beams also enhance resolution to the millimetre scale through matched filtering methods, so that echoes from smaller targets, such as copepods, can be extracted and tracked *in situ* at short range. Enhanced resolution enables target tracking algorithms for single individuals to perform better when particle density is high, thereby permitting behaviour studies of individuals inside schools or patches (e.g. Handegard, 2007). Ping rate operated during cruise transects determines the resolution of sampling. For example, patches of zooplankton and juvenile fish may be small (Benoit-Bird *et al.*, 2013) and a high ping repetition rate might be needed to properly resolve their distribution. Importantly, under such circumstances, plankton nets sample volumes far larger than the patches and, therefore, will not provide an accurate picture of the spatial distribution of the organisms that they capture.

Temporal resolution. High temporal resolution can be obtained by increasing ping rates during cruise transects, yielding enough pings on individuals or groups to resolve their distribution and behaviour patterns. In deep water, ping rate is limited by the travelling time of sound back and forth to the bottom or to the maximum survey depth. Ping rate may also be increased by using multi-pulse techniques that code the transmitted signal to allow several pulses to be used simultaneously. Long-term data for studying and quantifying important biological processes such as diel or seasonal cycles (Figure 2) or climate impacts on marine life require stationary systems (Genin *et al.*, 2005; Godø *et al.*, 2005; Kaartvedt *et al.*, 2009).

Identification by species and size is a key challenge for MEA**.** Identification of the targets in acoustic records has, to date, been dependent on simultaneous sampling using capture gear. Such sampling is now being improved through visual techniques that continuously image individuals during trawling, thus resolving observation over the depth range sampled (Deep Vision, Rosen and Holst, 2013). This might become an important technique for development of identification methods for independent acoustic remote sensing. Such methods can improve realism in assessment through continuous and accurate acoustic species identification. Some of the acoustic technologies available to accomplish this are described below.

Fisheries acoustics has moved from single frequency to multiple frequency analysis (Trenkel *et al.*, 2011) to exploit the emerging methods to identify single species or taxonomic categories of species (Horne, 2000; Kloser *et al.*, 2002; Korneliussen and Ona, 2002; Lavery *et al.*, 2007; Korneliussen *et al.*, 2008) and the size of individuals (Johnsen *et al.*, 2009) without the need for capture sampling. The recent development of quantitative scientific broadband systems will enable comparison of acoustic backscattering over a more continuous frequency spectrum. This will greatly improve the possibility to categorize targets to the level of species or taxonomic groups (Stanton, 2009; Lavery *et al.*, 2010; Stanton *et al.*, 2010). The richer information from individual targets that are present in the broadband echo can also be used to extract target size. Extending bandwidth towards lower frequencies (500 Hz to 20 kHz) enables studies of swimbladder resonance phenomena in fish as a tool for size and species identification (Holliday, 1972; Love, 1978; Løvik and Hovem, 1979; Jagannathan *et al.*, 2009; Godø *et al.*, 2010). Split-beam technology is useful, not only for spatial resolution (see p. 10), but also to allow identification of individual size through analysis of acoustic target strength using target strength–length relationships obtained empirically. In some cases, behavioural characteristics of the target can also aid in species identification.

Abundance/biomass. Acoustic backscattering can be converted into biomass and making such measurements for relatively long periods can provide insights into biophysically coupled processes. However, some basic technical issues must be solved before

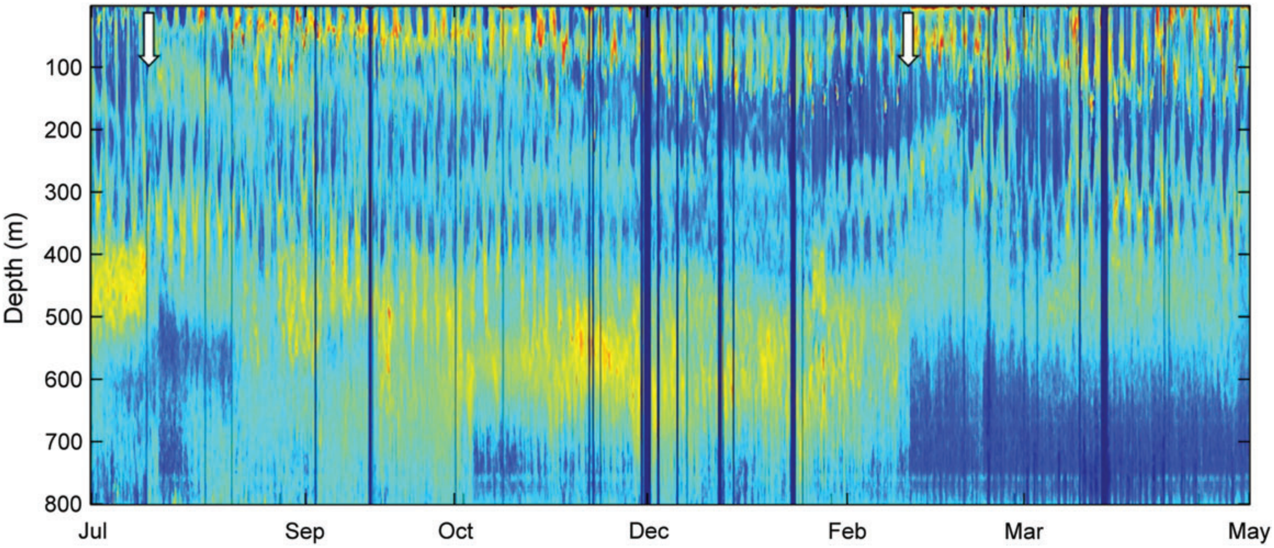


Figure 2. Seasonal variation in acoustic backscatter (smoothed over time) at a location on the Mid-Atlantic Ridge. Data are collected according to a mission plan leaving gaps of days between observations. Abrupt changes taking place in August and February – March (arrows) are probably caused by physical – biological influences on the acoustic backscatter associated with the movement of the Sub Polar Front (Opdal *et al.*, 2008) over the position of the acoustic unit.

meaningful biomass and process information can be obtained from acoustic backscattering.

As for any sensor technology, very careful calibration of instrumentation is required to obtain quantitative information from acoustics (Foote *et al.*, 1987, 2005). Careful and frequent calibration allows for measurements to be compared over time and among vessels or other acoustic platforms. Backscattering of marine organisms is affected by the orientation of the target, more so at higher frequencies than at lower. In other words, the behavioural characteristics of the recorded individuals affect the density measured. Normally, an average orientation is assumed. MEA aims to improve the measurement of backscattering by developing behaviour models that relate variation in fish behaviour to variation in backscatter (Holmin *et al.*, 2012). This will reduce the variability of the density measurements. The tools for doing this are improving continuously, as exemplified by the recent calibrated multibeam sonars and enhanced resolution in target tracking by split-beam broadband acoustics (Stanton, 2009; Ona *et al.*, 2011). A basic requirement for acoustic density estimation is knowledge of acoustic target strength. The enhanced resolution and modelling possibilities described above create a strong framework for *in situ* observation of target strength for taxon of smaller sizes and at higher densities.

Processes. Under MEA, a combination of the technology, tools, and approaches described above will permit systematic observation and quantification of processes such as species and trophic interactions and biophysical coupling. Although advances in acoustics have taken place with varying motivation and goals, they clearly demonstrate the potential of the technology with respect to the main issues—detection, identification, and enumeration. There are, however, challenges and difficulties that must be surmounted before these new technologies can be applied to full effect. These are taken up next.

Operational skills

Most of the acoustic technology solutions described above are typically operated from vessels. This creates operational limitations such as the extent of spatial and temporal coverage possible during surveys. Also, the use of higher frequencies limits the range of acoustic sampling since higher frequencies sample only a limited depth when vessel-based. Thus, to achieve the MEA objective of sampling on spatial and temporal scales relevant to the processes being observed, a suite of vessel- and non vessel-based platforms is required.

Below we describe how advanced operational solutions can compensate for inherent limitations in the acoustic technology and, thereby, permit us to sample at high spatial and temporal resolutions.

The vessel has been, and will probably remain, the single most important platform. In particular, the capabilities of research vessels to effectively operate alternative platforms, as described above, will be crucial. Further, fishing fleets are becoming advanced acoustic platforms (Karp, 2007). New vessels are occasionally designed with input from scientists so that they are essentially acoustic research vessels with respect to technology, noise characteristics, and laboratory, office, and cabin space. Involvement of the fishing industry in assessment and management of marine resources is both a political objective and an operational necessity to meet the requirements of EBM.

Vessel operated tethered platforms such as towed vehicles and profiling devices operate over large bandwidths and cover the whole depth range with identical volumes and bandwidths. They are powerful tools for uniform acoustic characterization of the water column. They can be towed or deployed vertically from a stationary vessel. Additional sensors, e.g. temperature/salinity and imaging cameras, can aid identification of organisms and the associated physical environment. Tethered systems operated from survey vessels overcome the range limitation of high frequencies and provide acoustic characterization of the full water column. These systems mirror or even surpass the performance of stationary and movable subsea platforms (described below), but are limited by the requirement for a vessel (Ona and Pedersen, 2012).

Stationary platforms allow for observations without the spatial confounding resulting from vessel movements. Sensors can be located anywhere in the water column depending on the process of interest. Such platforms are equipped in a manner similar to profiling platforms but normally with fewer frequencies. They support the collection of information on temporal variability on scales of seconds to years. Thus, they might become important tools for assessing the impact of climate change. Multiple examples of stationary systems that produce high temporal resolution data at depth exist, both anchored buoys (Doksæter *et al.*, 2009) and cabled bottom-mounted systems (Godø *et al.*, 2005; Kaartvedt *et al.*, 2009; Urmy *et al.*, 2012; http://love.statoil.com). Typical applications for such systems are quantification of processes such as diel rhythms in vertical migration, predator–prey interactions, swimming speed (Klevjer and Kaartvedt, 2011), tail beats and phase (Handegard *et al.*, 2009), and changes in acoustic properties of target species over time.

Autonomous moving subsea platforms are systems that collect acoustic data with advanced technology and transfer them in real time or near real time to a nearby vessel or data centre. They can be surface or submerged drifters equipped in a manner similar to stationary systems. They can also be autonomous underwater vehicles (AUV) with their own propulsion and navigation systems. Due to high power consumption and limited battery capacity, these platforms are most often used in experimental work of limited duration. Typically, they are used in studies of fish behaviour (e.g. vessel-induced behaviour), or studies of biophysical coupling or other studies requiring high spatial resolution. The transducers may point in various directions and collect data over various depth ranges according to the objectives of the study, and may include organisms that are inaccessible to most other sampling techniques (e.g. under ice—see Brierley *et al.*, 2002). Typically, such platforms can support observations of density distribution patterns and the behavioural characteristics of surface organisms that are distributed, for example, in a vessel's "blind zone" (e.g. herring and mackerel feeding at surface above the vessel transducer depth).

Oceanographic platforms like moorings and floats may host acoustic sensors. They must be designed without compromising the quality of biomass measurements, although they have size restrictions allowing only use of higher frequencies with associated range limits, and power limitations restricting sampling rates and operational lifespan (although advances are on the way here too). The capital and operating costs will be much lower than traditional systems and, therefore, they can be deployed in large numbers allowing high spatio-temporal coverage. The development of this category of acoustic platform is currently lagging behind some of the others and, as a result, these platforms are not yet commonly used for biological/ecological studies. Nevertheless, such platforms might become an important tool to enable relevant monitoring of oceanic ecosystems (Handegard *et al.*, 2012b). They are suitable for systematic vessel-based monitoring and/or specific process studies. Oceanographic acoustic platforms support two important roles in future monitoring. First, reduced purchase and operational costs makes spatial coverage realistic through a launch programme similar to the Argo buoy floats (http://www.argo.ucsd.edu/). Second, they enable simultaneous collection of physical and biological information over long periods of time, which is required to provide observational input to complex ecosystem process models.

The potential of acoustic sensors cannot be realized without exploiting the opportunities offered by advanced operational skills. The resulting data stream elevates the complexity of the data to a level that makes interpretation and utilization difficult. To compensate for this, a modelling approach is mandatory. This is elaborated upon in the next section.

Modelling

Modelling not only secures the integrity and consistency of the "big data" collected using acoustic technology, but also represents the common frame of reference for the multidisciplinary work taking place under the MEA concept: modellers will challenge the technology components with their specific needs for data with which to parameterize the simulations and new opportunities in acoustic technology will drive the development of modelling. MEA's ambition is to ensure that field data are collected and treated so as to satisfy the requirements of advanced ecosystem models.

The ecosystem oceanography component of EBM requires models linked to observations on the ocean's biological and physical characteristics (McClatchie *et al.*, 2012), and on a wide range of spatial and temporal scales. MEA incorporates this through active model development that exploits the opportunities offered by acoustics and, conversely, by employing models to direct technology development. Two basic challenges associated with the MEA concept can be solved through modelling. First, it is a basic challenge to set up a flexible monitoring programme that spans the wide range of spatial and temporal scales that it is now possible to sample with acoustic technology. Second, EBM requires quantitative understanding of ecosystem dynamics and processes as a foundation for integrated assessments (Link and Browman, 2014). A simple example is how predator–prey interactions between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) are assessed from combined acoustic-trawl information in the Barents Sea. The collected stomach data of cod and the information on distribution overlap of the two species is used as a basis for advice on total allowable catches assessing impacts on stocks from both fishing and predator–prey interactions (Bogstad and Gjøsæter, 2001; Johannesen *et al.*, 2012).

The MEA approach offers opportunities to observe ecosystem dynamics and properties across a wide range of temporal and spatial scales. For example, temporal fine-scaled observations (e.g. individual fish behaviour) usually span a limited spatial scale, whereas observations on coarse temporal scales span larger spatial scales (e.g. satellite data) with crude resolution. An associated challenge is that fine-scale observations are resource demanding and wide geographical coverage is neither practically achievable nor economically viable. To address this, intercalibration and integration of observations across sensors and platforms require tailored models to infer the role of the fine-scale (time and space) processes on larger scales [see citation of Levin (1992) above]. This can be achieved using statistical models, where the fine-scaled observations are (ideally random) subsamples of the large-scale system, and proper survey designs combined with modelling can combine information over the relevant spatial and temporal scales. One specific example is the potential to combine stationary acoustics with acoustic observations from transects. Modelling diel impact on density distribution patterns of marine organisms from the stationary observations and adjusting the transect data therefore will enable separation of spatial and temporal distribution impacts; a basic requirement for understanding ecosystem function. Additional usage of unstructured data from "ships of opportunity" may greatly expand the pool of observations (Handegard *et al.*, 2012b). Further, to obtain a quantitative understanding of ecosystem dynamics, the tailored observation-modelling framework of MEA needs models that fully utilize the observation systems. The amount of information available from the various types of platforms and acoustic sensors goes beyond what can be handled by existing models, and further development of models that respond to the potential of new observations is essential. Similarly, acoustic observation approaches must be developed according to the needs of models, including both testing of assumptions and estimation of model parameters.

Models can be built to inform integrated assessment needs of an ecosystem, similar to that of traditional stock assessments models to set fishing quotas, where the observations can be assimilated with the models and used to predict key properties for the assessment. However, the concept goes beyond parameterization of models relevant to the assessment. By implementing competing hypotheses of ecosystem processes, the models can be used to predict the observations which enable testing of the contrasting hypotheses. This will, in turn, provide understanding of the key processes in the ecosystem and eventually ecosystem function.

We have emphasized that full utilization of the data collection in MEA cannot be realized without a strong modelling component. Modelling for EBM requires a tight interaction with the assessment and management community and cannot be specified in general terms under MEA. Such interaction is essential to secure that models produce useful information and, *vice versa*, so that the assessment and management community is made aware of the potential of MEA to generate relevant data and validate models.

Case studies demonstrating the strength and potential of the MEA approach

The credibility of a new concept/approach to a research question requires demonstrations that illustrate its viability and realism. We have chosen some basic challenges associated with EBM to demonstrate that flexible solutions combining *acoustic technology* with *operational skills* and *modelling*—that is, MEA—can move fisheries oceanography beyond what has been possible using capture technology.

Understanding productivity-determining processes and ecosystem function

"What we cannot do is describe the world in the absence of any prior understanding of it, and in the absence of any theory" (Harré and Secord, 1972, p. 163). Our ability to describe the underwater world is basically expanded with MEA as a tool for understanding ecosystem function through insight into processes at all scales from individual behaviour to meso- and large-scale circulation dynamics. In this example, we want to illustrate that acoustic technology enables collection of wide range of data which supports understanding of ecosystems but which currently are given limited attention by ecology and modelling.

Physical–biological coupling is a basic driver of ecosystems. Since acoustics images distribution patterns in the sea as they occur, it can provide insight into such interactions. For example, vessel-based and moored echosounders image internal waves and thin layers which influence the distribution patterns of plankton and, therefore, the larger organisms that prey upon them (Holliday, 1972; Farmer and Armi, 1999; Benoit-Bird, 2009; Kaartvedt *et al.*, 2012). At larger scales, Godø *et al.* (2012) demonstrated how vessel-based acoustics enables mapping of the density structure in mesoscale eddies and how the phenomenon shapes the ecosystem and stimulates higher trophic marine life: the physical concentration of food or food production produces a habitat for higher trophic levels that otherwise would not exist. Similarly, Zwolinski and Demer (2012) and Zwolinski *et al.* (2011) demonstrate how acoustics and associated oceanographic observations can be used to characterize the pelagic habitat of fish in the Californian current.

Patchiness of organisms determines predation success and survival of organisms at higher trophic levels, but traditional net sampling techniques are unable to assess the real size of patches and their distribution in time and space. Knowledge of such patterns is crucial to build basic understanding of how these distribution patterns cascade through higher trophic levels as demonstrated by several studies using acoustics (Ressler *et al.*, 2012; Benoit-Bird *et al.*, 2013).

Predator–prey interactions are another basic ecosystem process where acoustics may support the generation of fundamental new knowledge. As an example, predator–prey interactions have been evaluated in the Barents Sea based on trawl-based point samples. Combining this with information from whale observations and seabirds allows for a better understanding of predator–prey interactions (Johannesen *et al.*, 2012). However, the predator–prey interactions are often fine-scale processes, and acoustics addresses this at more appropriate scales than trawl indices, not least due to the vertical resolution offered. This is exemplified through whale–herring interactions (Nøttestad and Axelsen, 1999), and also simultaneous recording of single individual *predators and prey* is possible with split-beam systems (Onsrud *et al.*, 2005) and high-frequency imaging systems (Handegard *et al.*, 2012a), demonstrating the potential of acoustics over more conventional approaches to resolve fine-scale trophic interaction processes. A good example of a predator–prey interaction process is the behavioural impact on small mesopelagic fish, the silvery lightfish (*Maurolicus muelleri),* in the presence of a predator. From a long-term study using a cabled submerged stationary platform with an echosounder, the vertical distribution of the small mesopelagic fish *M. muelleri* was observed to change dramatically and very rapidly in response to a predator. An example of this reaction is shown in Figure 3—a scattering layer ascribed to juveniles of this species descends tens of metres upon encountering predators. Further, the vertical distribution of *M. muelleri* has been studied extensively, with acoustic observations revealing a clear relation to light levels (Giske *et al.*, 1990; Balino and Aksnes, 1993; Staby and Aksnes, 2011). Subsequent modelling has addressed the vertical distribution in terms of trade-offs between feeding and predation risk, both being expressed in terms of the light conditions (Rosland and Giske, 1997; Staby *et al.*, 2013). These long-term acoustic observations suggest that additional variables may be included which can be quantified through observations, exemplifying the potential of the coupled modelling–observation approach. Similarly, acoustic observations have revealed whales feeding on mesopelagic fish (Figure 4, Benoit-Bird and Au, 2009a, b; Godø *et al.*, 2013).

Understanding the drivers of variability in fish stock recruitment

Recruitment to most large fish stocks is thought to be determined by a combination of predation, starvation, and displacement away from appropriate nursery grounds during the early life history stages (e.g. Houde, 2009). With the observation capabilities described above, and the resolution possibilities described for the acoustic technologies, MEA observation methods can be tailored to not only observe interactions between fish larvae and copepods, and fish larvae and their predators, but also to quantify these interactions using broadband and split-beam technologies. This would

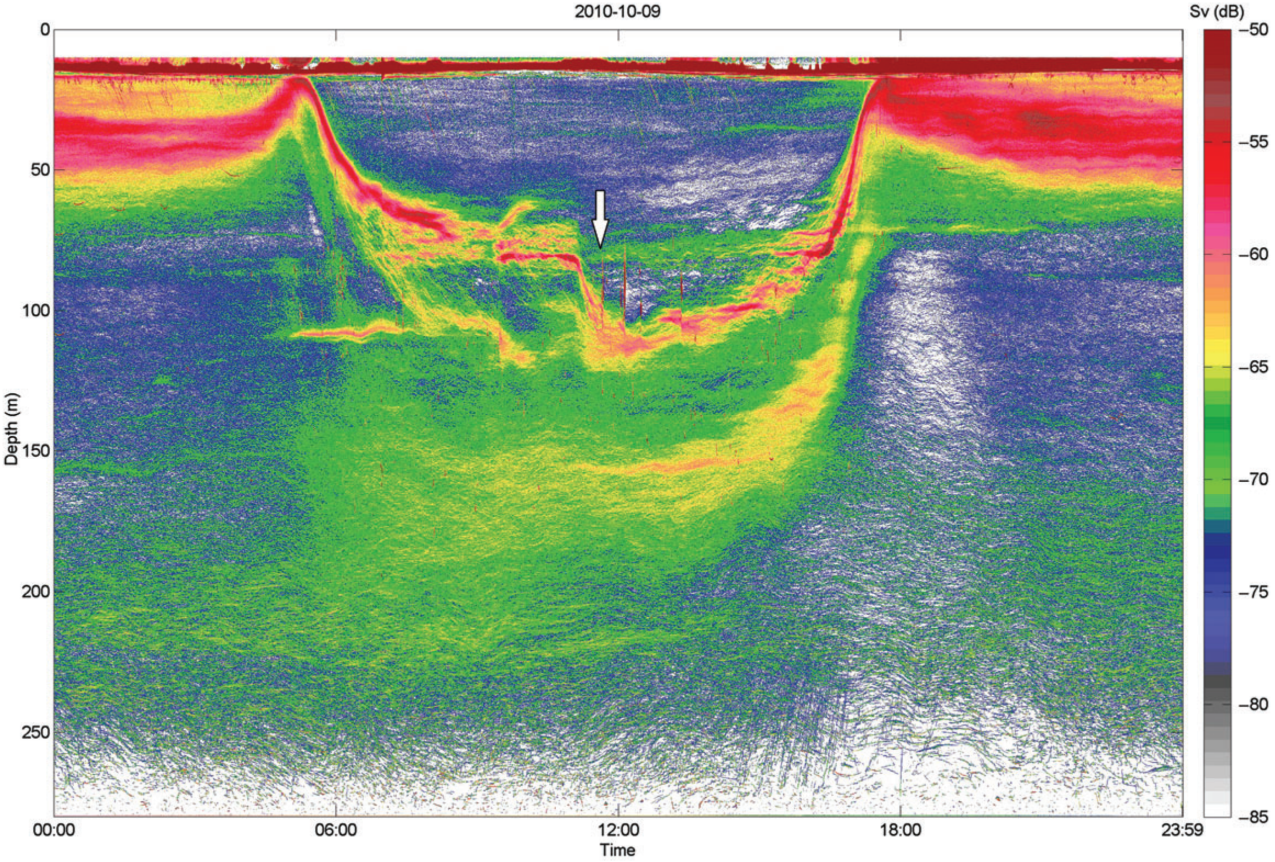


Figure 3. Echogram capturing the diel vertical migration of a small silvery lightfish (*Maurolicus muelleri*) layer impacted by schools of predators (white arrow) at 100 m depth at about 12:00 UTC. Note how the depth distribution of prey changes substantially after contact with the predator.

be facilitated by interpreting the movement patterns observed acoustically with fine-scale observations made in the laboratory (e.g. Browman and O'Brien, 1992; Abrahamsen *et al.*, 2010; Browman *et al.*, 2011; Vollset *et al.*, 2011). Further, with operational skills as a tool for designing a sampling regime for larvae during the period from first feeding to the nursery grounds, essential information for quantitative drift models, which are currently based upon assumptions, can be assessed (see Johansen *et al.*, 2009). Such a distributed intensive sampling programme is becoming realistic through the utilization of low-cost oceanographic platform acoustics. Attempts to predict distribution patterns of larvae based on such particle models fail if they do not consider behavioural aspects (Johansen *et al.*, 2009; Ospina-Alvarez *et al.*, 2012; Sundelof and Jonsson, 2012; Staaterman and Paris, 2014). In a long-term perspective, when quantitative observations of behavioural characteristics with appropriate resolution through tailored technology are possible, and these are combined with models, it will be feasible to more thoroughly and realistically test the prevailing hypothesis of Hjort, Cushing, and others (reviewed by Hare, 2014).

Censusing fish stocks using MEA

Assessing fish stocks using acoustics requires precise abundance measurements and correct identification of the acoustic traces. Both issues belong to the basic acoustic technology solutions described above. Identification is currently done predominantly by trawl sampling. Trawls accumulate information over large volumes and provide neither species nor size information at the spatial or temporal scales provided by acoustics. A renewal of fish stock assessment therefore requires further development of acoustic identification techniques, so as to avoid degradation of acoustically measured details by crude resolution and selective trawls. The acoustic probing platform with built-in optical instruments for identification and the Deep Vision trawl system (mentioned above) are examples of how the identification challenge can be addressed.

Acoustic-trawl surveys combine information from net sampling and acoustics to generate indices of abundance that are used in stock assessment (Aglen, 1994). Challenges for a well-designed survey are often associated with biased observations caused by various processes (Godø and Wespestad, 1993), including relative changes in sampling gear selectivity, acoustic blind zones (Totland *et al.*, 2009), vertical distribution, and avoidance behaviour of the focal species (Olsen *et al.*, 1983; De Robertis and Handegard, 2013). As an example, new scientific sonars and modelling efforts that combine detailed sonar information with a behaviour model before combination with echosounder data are promising, as discussed by Holmin *et al.* (2012). Such approaches may provide a platform for merging the data from the various sensors and ultimately help overcome some of the obstacles associated with interannual variability in survey indices.

Implementing MEA

Present marine research and monitoring employs a combination of acoustic technology solutions and simple operational skills to

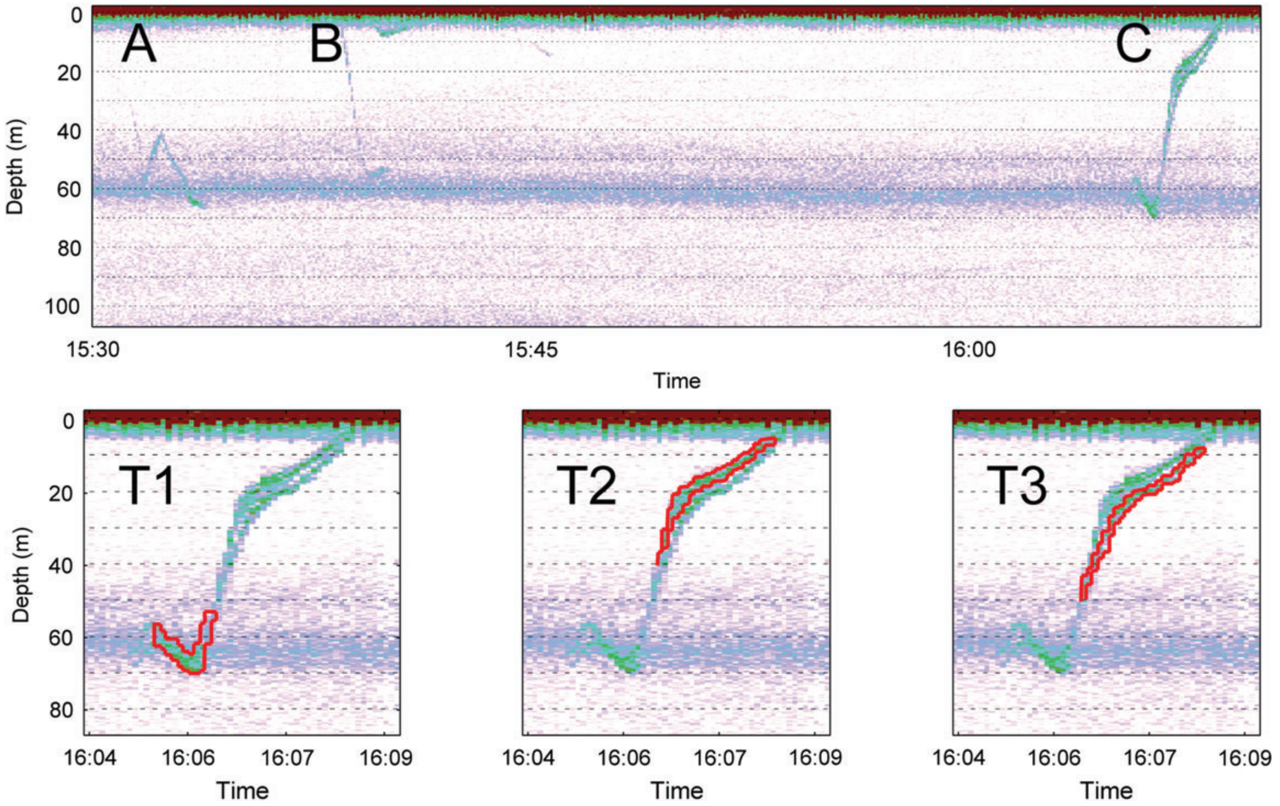
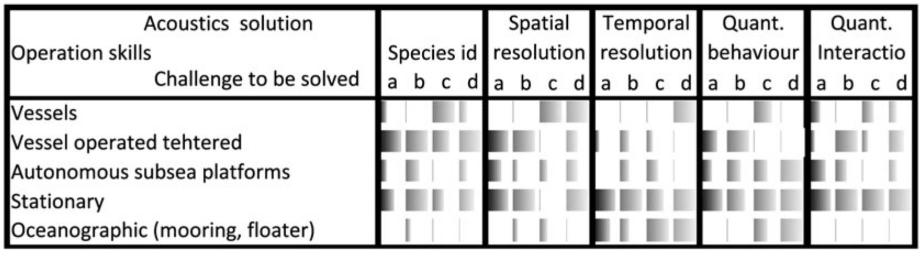


Figure 4. Whale diving behaviour as recorded by stationary acoustics. Upper panel: Echogram capturing layer of mesopelagic fish at 60 m depth and diving whales recorded as vertically moving traces (A, B, C). Lower panel: Details of whale track C. Red boxes show the separated track as indicated by target tracking algorithms. The black marks identify accepted single targets according to the detection criteria defined for the algorithm. The red box in T1 indicates a single individual, whereas separation of the signal into two individuals occurs in the red boxes of T2 and T3. The tracks in T2 and T3 probably refer to detected density differences when the acoustic signals pass into and out of the whale body. The distance between them thus reflects the size of the animal [the figure is adopted from Godø *et al.* (2013) where further details can be found].

Table 1. A schematic illustration of how combinations of acoustic solutions and operational skills can support some of the key challenges of ecosystem-based management (EBM).



Acoustics solution Operation skills Challenge to be solved	Species id a b c d	Spatial resolution a b c d	Temporal resolution a b c d	Quant. behaviour a b c d	Quant. Interactio a b c d
Vessels					
Vessel operated tehtered					
Autonomous subsea platforms					
Stationary					
Oceanographic (mooring, floater)					

The key challenges of EBM are grey scale-coded, with the size of the grey bar in each cell indicating the importance of that specific combination of acoustics solution and operational skill to solve the given challenge. The grey scale coding scheme is: ecosystem function, a; fish stock recruitment, b; fish stock assessment, c; ecosystem assessment, d. For example, stationary platforms provide high temporal resolution (horizontal bar covers the column) of importance to fish stock recruitment (identified by size of bar in column b).

address the needs of fisheries science, marine ecology, and EBM (Table 1). A stronger reliance on acoustic systems, combined with an expanded and designed use of operational systems—that is, MEA—is required to meet the challenges presented from the left to the right side of each cell in Table 1. Implementation–operationalization of the MEA concept would occur as follows:

(i) Establish an operational data storage and processing framework that enables accessibility and merging/fusion of information at the various spatial and temporal scales. This is a prerequisite for the MEA approach and requires immediate action to ensure that existing data can be used to efficiently develop new concepts.

(ii) Define the variables that must be observed, and at what temporal and spatial scales, to understand and model productivity-determining processes. This step must be implemented in close cooperation with ecosystem modellers to ensure that the information produced, and its format, can be readily input into models.

(iii) Following from (i), develop and deploy observation systems (combinations of acoustic solutions × operational systems) and ensure that the data that they produce are relevant to, and useful for, biophysically coupled ecosystem models. Here, it is essential to start with clear priorities based upon existing knowledge (or the lack thereof), keeping in mind Levin's (1992) statement about "...retaining essential information without getting bogged down in unnecessary detail".

(iv) Evaluate and adjust the observation framework according to the outcome of (i)–(iii) and improve the cost-efficiency of observation systems by developing a dynamic interaction between the quantitative observation and modelling framework.

(v) Establish a long-term monitoring framework that includes observation systems, operational infrastructure, operational routines/procedures, and models that permit data production and analysis that follow from the needs of EBM.

(vi) Develop cross-disciplinary educational programmes that produce scientists with the required knowledge and skill so that MEA's three components can be seamlessly integrated.

Clearly, achieving all the above will require a systematic approach in more than one institution and will not occur overnight. However, the potential in the approach justifies the effort that will be required to make it a reality.

Concluding remarks

A basic challenge of both fisheries science and ecology, and something that is at the heart of successfully implementing EBM, is empiricising productivity-determining processes, biophysical coupling, and trophic interactions (see, for example, North *et al.*, 2009). Observing such processes—at the spatial and temporal scales on which they occur—is impossible with classical observation methods but is within our grasp with existing acoustic technology (Godø, 1999; Beamish and Rothschild, 2009). Numerical models of ecosystem processes have also made great advances but are missing an empirical basis (e.g. Peck *et al.*, 2012; Peck and Hufnagl, 2012; Griffith and Fulton, 2014). Coupling the acoustics-based observational capacity with ecosystem modelling is the raison d'etre of the MEA approach.

Fisheries science and marine ecology have developed independently in support of different scientific questions and objectives. However, fisheries science needs ecology to meet the requirements of EBM. Concurrently, these challenges from fisheries science will improve the empirical base used to test the core concepts and hypotheses of marine ecology and fisheries oceanography (see Hare, 2014). Thus, by necessity, EBM is forcing fisheries science towards a closer connection with marine ecology and fisheries oceanography. The MEA approach would provide a foundation that would drive basic steps forward for both fields and will stimulate more interaction between them. MEA could also reduce the gap between terrestrial and marine ecology (see Stergiou and Browman, 2005) by decreasing the current disparity in observation abilities in terms of space–time resolution between terrestrial and marine environments. In this sense, MEA would represent a breakthrough in fisheries science and marine ecology.

Acknowledgements

We thank Dr Michael Jech and Dr Brian Marcotte for comments and suggestions on the manuscript.

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Handling editor: David Demer