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Studying spatial and trophic interactions between capelin and cod using individual-based modelling

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The objective of this study was to use spatially explicit individual-based models for simulating the movement, foraging, growth, and mortality of cod and capelin in the Barents Sea in order to identify general features in their migration patterns and the consumption of capelin by cod. The individual-based models are initiated from survey data run over 1 year and validated against survey information. Directed movement is based on a combination of movement vectors and temperature boundaries, and bioenergetics models are used to calculate growth. Capelin consumption by cod is calculated from local encounters between the species. For capelin, the best movement model can be summarized as: stay southwest of the 2.5°C and 4°C temperature front at 50-m depth for juvenile and mature individuals, respectively, in winter, and migrate northwards during summer, but do not pass the −1.5°C temperature front. The best cod model was to migrate south-southwest during winter and north-northeast during summer, within the temperature range 1°C to 8°C. The annual consumption estimates found here reflected the interannual and seasonal pattern from previous studies based on stomach samples, but were generally lower. Consumption estimates varied depending on the movement models, and the best movement model also produced the consumption estimate closest to that obtained in other studies. Introducing a simple rule stating that cod should move in a randomly selected direction when the local capelin density is zero increased the consumption estimate by 30%. This suggests that more emphasis needs to be put on exploring how behavioural rules in predators and prey affect their interactions. Even though there are some discrepancies between predictions and observations, the results achieved by the model with regard to spatial distribution, growth, and consumption are promising.

Keywords: Barents Sea, bioenergetics, capelin, cod, consumption, individual-based modelling, migration, predator and prey.

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Introduction

Predator–prey interactions are of great importance in fisheries research, particularly as we attempt to move away from management of marine resources based on single-species assessments towards an ecosystem-based approach. Spatial overlap between predator and prey is a prerequisite for predation to occur. Consequently, it is important to address spatial processes in order to understand and enable quantification of predator–prey interactions (Magnússon, 1995). In general, fisheries assessment models are highly aggregated with regard to space, time, and biological detail in order to allow parameter estimation. Consequently, such models are not designed to study species interactions. Notable exceptions are multispecies models, which have been developed to address the impact of species interactions on the population dynamics of fish (Helgason and Gislason, 1979; Pope, 1979; Bogstad *et al.*, 1997; Stefánsson and Pálsson, 1998). However, such models generally use large spatial and temporal scales, and thus the modelling of processes such as predation, growth, and migration is rather coarse. Here we approach species interactions from a different modelling philosophy by using individual-based models with a fine spatial resolution and short time-steps to simulate the movement, growth, and survival of cod (*Gadus morhua* L.) and capelin (*Mallotus*

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villosus Müller 1776) in the Barents Sea. The consumption of capelin by cod emerges from simulating encounters between the two species, and growth is calculated using bioenergetics models.

The interaction between cod and capelin is considered a key process in the structuring of many boreal marine ecosystems (Rose and Leggett, 1990; Hopkins and Nilssen, 1991; Vilhjálmsson, 1994; Bogstad *et al.*, 2000; Rose and O'Driscoll, 2002). This relationship is a classic example of predator–prey interactions involving both behavioural (Fiksen *et al.*, 1995; Huse, 1998) and numerical responses (Hopkins and Nilssen, 1991; Bogstad *et al.*, 2000). In the Barents Sea, the geographical distribution of the capelin is closely associated with the ice edge throughout large parts of the year. During summer, the capelin follow the retracting ice edge and prey on the secondary production in the rich marginal ice zone (Hassel *et al.*, 1991). As winter approaches, the capelin migrate towards the central parts of the Barents Sea for over-wintering (e.g. Hamre and Monstad, 1980; Gjøsæter, 1998). In spring, the mature capelin migrate to the coasts of Northern Norway and the Kola Peninsula in Russia, where they spawn. The spawning migration of capelin and the subsequent location of the spawning grounds are related to the prevailing climatic conditions (Ozhigin and Luka, 1985). Even though cod predation on capelin takes place throughout the year there is a pronounced peak in spatial overlap and predation during capelin over-wintering and spawning (Mehl, 1989; Mehl and Sunnanå, 1991; Dolgov, 2002).

Information on the spatial distribution of cod and capelin is provided mainly from biannual surveys performed approximately 6 months apart. This level of temporal resolution is insufficient for understanding the interaction between these populations. Increasing the frequency of surveys would be the best way to improve our knowledge of the spatial dynamics of cod and capelin, but this is costly. An alternative way to address this issue is to build models that take into account movement dynamics as well as trophic interactions. This can be achieved by using individual-based modelling which allows ready inclusion of movement behaviour, spatial detail, and individual interactions. The Barents Sea ecosystem is relatively simple with few species at each trophic level. While this renders the system prone to fluctuations, it also makes it well suited for model development.

Fish migrations are based on utilizing the environmental heterogeneity and seasonality in order to optimize conditions for different life stages. We do not pursue the ultimate causes for the migrations of cod and capelin, but rather focus on describing the migrations and the consequences for the interaction between the species. The objectives of this study are: (i) to use simple movement models to identify general features in the migration patterns of cod and capelin; (ii) to simulate foraging, growth, and mortality of the species' interaction with the environment and each other; (iii) to investigate how growth and survival of the two species and cod's consumption of capelin are affected by different migration patterns; (iv) to evaluate spatially explicit IBM as a tool in fisheries research.

Material and methods

The individual-based model

For a general introduction to IBM, see DeAngelis and Gross (1992), Grimm (1999), or Huse *et al.* (2002). Fish populations can be represented in IBM by using super-individuals (Scheffer *et al.*, 1995). A super-individual represents many identical individuals, here referred to as siblings. This is an efficient way to maintain the individual-based structure, and still be able to simulate the large population sizes that occur in fish populations. An attribute vector **AV** (Chambers, 1993) is applied to keep track of the states used to specify super-individuals. Mortality operates on the super-individual and number of siblings of super-individuals is thus decreased in proportion to the mortality rate. The following attribute vector was here used for cod and capelin:

$$\mathbf{AV} = (\mathrm{a}, \mathrm{l}, \mathrm{w}, \mathrm{n}, \mathrm{x}, \mathrm{y}) \qquad (1)$$

where a is age, l is length, w is weight, n is the number of identical siblings, x and y are spatial positions of a super-individual. The model domain consists of a 90 (x-axis) by 100 (y-axis) grid of 20 × 20 km squares (Figure 1). The observations were initiated from survey data (see below) as average length and weight, and number of each age group in the squares. Each age group in each of the squares with observations was initially allocated a super-individual, with length, weight, and internal number corresponding to the observations for that square. After all the observations had been allocated to super-individuals, new super-individuals were generated from the existing ones until each of the two populations consisted of 20 000 super-individuals. This was performed by picking the most abundant super-individual (donor), and generating a new one by copying the attributes of the donor. The abundance was then divided by two, both for the donor and the new super-individual to maintain mass balance (Rose *et al.*, 1993). The number of super-individuals is a trade-off between having a high resolution of the population, but at the same time keeping computer running time within reasonable limits. Daily time-steps were used.

Temperature

Temperature data for 1990–1996 were taken from a digital temperature atlas for the Barents Sea based on hydrographic measurements from the Institute of Marine Research (IMR, Bergen, Norway) at different, spatially referenced locations. The average temperature in the upper 200 m was used as an estimate of capelin ambient temperature, since this is the regular range of capelin vertical distribution

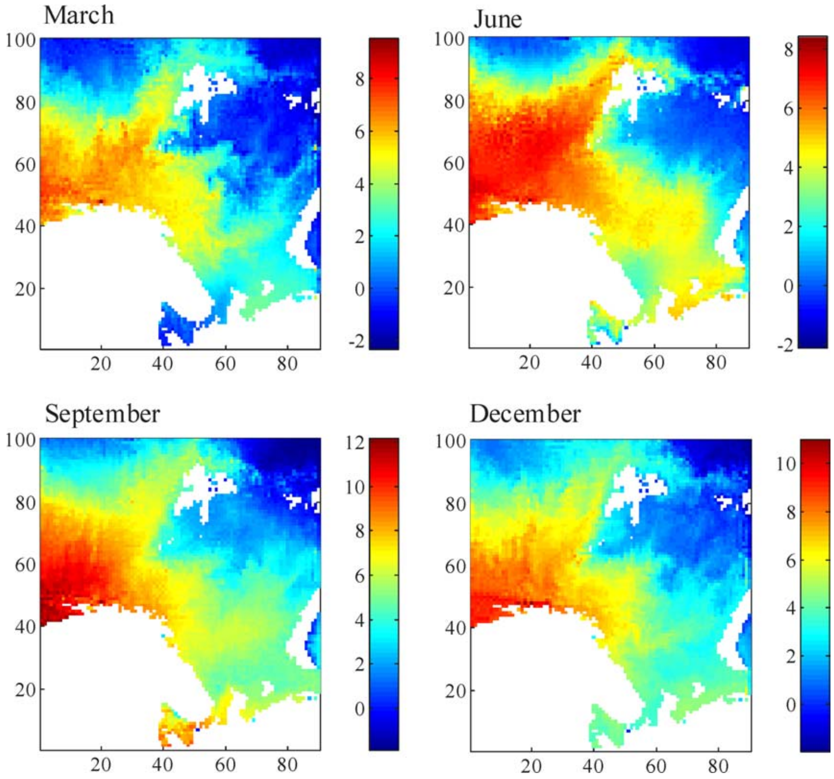

Figure 1. The model domain with simulated surface temperature distribution for four different months during 1990 (December) and 1991 (March, June, and September). The values given in the legend are surface temperatures in °C; the white areas are land.

(Gjøsæter, 1998). For cod, the average temperature in the range 100–200 m was used since cod is characterized as a demersal fish and generally dwells deeper than capelin. The temperature data were converted to the regular polar stereographic grid constituting the model domain. The data were spatially interpolated in each depth strata using a partial spline interpolation method based on nearest neighbours in the G3GRID procedure in the SAS® software package. Before interpolation, temperature fields generated by an ocean circulation model (Ådlandsvik and Sundby, 1994) were used to provide temperature data in grid cells at the edge of the temperature atlas, to control for boundary effects caused by the spatial interpolation technique. Simple temporal interpolation between measurements in the third and the first quarters of the year were performed to obtain daily temperature fields. This was done because of the greater sampling frequency in these quarters compared with the other two quarters. The Kola section in the Barents Sea (70°30′N to 72°30′N along 33°30′E; Tereshchenko, 1996) is measured monthly. There are fairly linear relationships between the monthly temperatures at the Kola section during the period September to March (linear regression, $p < 0.001$, $r^2 = 0.99$) and from March to September (linear regression, $p < 0.001$, $r^2 = 0.92$) for the monthly average temperatures in the 6-year study period. This supports the use of linear interpolation between the third and the first quarters, corresponding approximately to September and March. The simulated surface temperature fields, which illustrate the magnitude of seasonal changes in temperature in the Barents Sea (Figure 1), were used in calculating fish advection, applying the same depth ranges for cod and capelin as used for temperature (see above). The current fields were generated by the ocean circulation model.

Survey data

Data from a survey in September–October (Gjøsæter *et al.*, 1998) were used to initiate the capelin super-individuals. The survey is an annual acoustic survey involving four research vessels from Norway and Russia. During this time of the year the capelin stock is distributed over wide areas of the northern and central Barents Sea and is undertaking vertical migrations. The capelin are not normally found near the surface or the seabed, and are therefore ideally distributed for acoustic stock estimation (Toresen *et al.*, 1998). The methods used and the results from the whole time-series going back to 1972 are summarized in Gjøsæter *et al.* (1998). Acoustic data on capelin were directly converted to the temperature grid. Biological information from hauls during the survey is compiled in a geographical block system (Gjøsæter *et al.*, 1998), and the average values from these blocks were used in initiating the capelin super-individuals.

Data from a demersal fish survey in August were used to initiate the cod super-individuals (Aglen, 1999). This survey is carried out using essentially the same methodology as the Norwegian survey for demersal fish in the Barents Sea in January–March (Jakobsen *et al.*, 1997). For cod, swept area estimates from trawl surveys were calculated within areas defined by strata systems used by IMR during standard bottom trawl surveys on demersal fish in the Barents Sea in winter and autumn. Number of individuals by age group was then estimated by scaling the swept area estimates with VPA estimates of the cod abundance (ICES, 2002) in the same way as done by Johansen *et al.* (2004). Cod distribution was determined using a combination of acoustic and bottom trawl data. Cod distribution data for 1994 are missing, and thus distribution data from 1995 were used for initiating the cod super-individuals in 1994. However, the abundance data were taken from the VPA for 1994. Abundance data for cod were converted to the same grid as the temperature and capelin data. The abundance data for cod were uniformly distributed on the grid cells within each stratum. The bottom trawl hauls are distributed with a distance of 20–40 nmi between each haul along regularly spaced survey tracks. The density of hauls is similar in the winter and autumn surveys, and varies between strata according to the expected density of fish, based on earlier survey results (Jakobsen *et al.*, 1997). In the strata system used in the winter surveys, the number of squares varies from 37 to 120 according to the size of the stratum, with a mean of 76 squares. In the autumn strata system, which generally has larger strata, the number of squares varies from 121 to 528, with a mean of 242 squares. Maps showing both strata systems can be found in Johansen *et al.* (2004).

In addition to the surveys in the Fall used to initiate the distribution, a winter survey in January–March (Jakobsen *et al.*, 1997) was used to validate the model predictions. This survey targets demersal fish, in particular cod and haddock. However, acoustic abundance of capelin is also recorded. It should be noted that the spatial coverage of this survey is limited by ice. Furthermore, the simulated distributions were compared with the cod and capelin distributions in the following Fall. Information on the spawning area of capelin in different years was taken from Gjøsæter (1998), and these data were used to evaluate the simulated spawning migration. Age groups 1–4 were studied for capelin and 2–10 for cod. As customary in fisheries science, age is updated on 1 January. Intervals of 0.5 and 5 cm body length were used for capelin and cod, respectively.

Growth and mortality

Growth (G) was modelled using bioenergetics models (Hewett and Johnson, 1992). A basic balanced energy budget is the foundation of such models:

$$G = C - (R + S + F + U) \qquad (2)$$

where C is consumption, R is respiration, S is specific dynamic action, F is egestion, and U is excretion. Each of the variables on the right-hand side of the equation was calculated by species-specific equations and parameters. The bioenergetics model for cod is described in Hansson *et al.* (1996). There is no similar model for capelin, and instead we used a bioenergetics model for herring documented in Hewett and Johnson (1992), as done previously by Fiksen *et al.* (1995). In addition to the species-specific parameters, the model relies on information about temperature and feeding level.

Capelin feeding is known to vary seasonally due to variable availability of zooplankton, and there is a peak in feeding during late summer (Lund, 1981; Gjøsæter, 1998). A relative measure of zooplankton biomass was generated by:

$$Z_{tj} = (T_{tj} + 2) \times S_t \qquad (3)$$

where Z_{tj} is the relative zooplankton abundance and T_{tj} is the temperature, in square j at day t. S_t represents the level of the zooplankton abundance at day t, due to seasonal variation. In order to avoid negative zooplankton abundance at negative temperatures, a constant was added. The seasonal component was implemented by a Gaussian curve with a peak in mid-July (Melle and Skjoldal, 1998), and a standard deviation of 18 days. A lower level of zooplankton abundance corresponding to 10% of the maximum abundance was set to take into account prey such as euphausiids and amphipods that are available throughout the year. During summer there is a bloom in the marginal ice zone of the Barents Sea as the ice withdraws and makes nutrient-rich waters available for planktonic production (Hassel *et al.*, 1991; Sakshaug *et al.*, 1992). This production was included by enhancing zooplankton biomass in the marginal ice zone (temperature range [0,1.5]°C) by 30% during July through September (Fiksen *et al.*, 1995). Consumption (Equation 2) is calculated as the product of a temperature-dependent function, an allometric relationship and the feeding level. The former two components are described in the documentation of the bioenergetics models (Hewett and Johnson, 1992; Hansson *et al.*, 1996). The feeding level, which is in the range [0,1], was calculated from the relative zooplankton biomass (Equation 3) using a Michaelis-Menton-like Equation (4) with a half saturation constant $KL \times Z_{max}$:

$$PL_{tj} = \frac{Z_{tj}}{(KL \times Z_{max} + Z_{tj})} \qquad (4)$$

Here, PL_{tj} is the feeding level of capelin in square j at time t, and Z_{max} is the maximum zooplankton biomass obtained in a square during the simulations. The half saturation constant was implemented as a fraction of the maximum zooplankton biomass (KL = 0.2; Fiksen *et al.*, 1995), giving the zooplankton abundance where the feeding level is half the maximum feeding level.

Cod was assumed to have a constant feeding level of other food (OF) in addition to the foraging on capelin, which depends on the local capelin density:

$$PC_{tj} = OF + \frac{NL_{tj}}{(KC \times NL_{max} + NL_{tj})} \qquad (5)$$

where NL_{tj} is the density of capelin in square j at time t, and NL_{max} is the maximum capelin density achieved in a square during the simulations. PC_{tj} was not allowed to exceed 1, and higher values were set equal to 1. $KC \times NL_{max}$ is the half saturation constant, and the default value of KC is 0.001. However, this parameter is investigated below. Cod foraging on capelin is calculated square by square in two steps. First, an initial estimate of the consumption of each cod super-individual is calculated by letting each super-individual feed sequentially according to the capelin density in the square, taking into account the reduction in capelin biomass caused by cod feeding. Then the biomass of capelin eaten by cod super-individuals in each square is summed. Next the total capelin consumption in the square is divided by the cod biomass in the square to yield an estimate of biomass of capelin consumed per biomass of cod, which is then used to calculate the total consumption by each cod super-individual. Following cod feeding, the internal number of capelin super-individuals in the square is reduced in proportion to the feeding of the predator. If several capelin super-individuals reside in one square, the mortality is distributed equally among them. In such cases, the average weight of capelin in the square is used to convert from number eaten to biomass. In addition to feeding on capelin, cod ingest invertebrates such as shrimp, amphipods, and euphausiids, as well as herring and polar cod (Mehl, 1989; Mehl and Sunnanå, 1991; Bogstad *et al.*, 2000; Johansen, 2002). The feeding level generated by other food was assumed to be 20% of the maximum feeding level (OF = 0.2). The size of this ration is a bit uncertain and is investigated below.

Two different values of body weight were used for cod and capelin: structural weight and present weight. Structural weight is a measure of the skeletal size, and is proportional to the length of the fish (Rosland, 1997). Present weight (w, Equation 1) is proportional to the individual's total energy content, and hence reversible. Positive growth increases the present weight, and if present weight increases beyond the structural weight, the structural weight is increased to the level of the present weight. In cases of negative growth, present weight is decreased, but the structural weight is unchanged. If the present weight is decreased below 50% of the structural weight, the super-individual dies.

The survival of cod siblings from time t to t + 1 is calculated by:

$$nc_{t+1} = nc_t \times e^{-\mu} \qquad (6)$$

where nc_t is the number of cod siblings in a super-individual at time t, and μ is the daily mortality rate. The daily mortality rate of cod was calculated by adding the year-specific VPA estimates of fishing mortality (F_{5-10}; ICES, 2002) and a natural mortality rate of 0.2. In addition, there is starvation as described above. There was a fishery for capelin during the first 3 years of the study period. The fishery mainly takes place during winter. Fishing mortality was implemented by ''harvesting'' at random from 3- and 4-year-old capelin super-individuals during February and March until a biomass corresponding to the landings (Toresen, 2000) was taken. A natural mortality rate of 0.2 was assumed for capelin in addition to the simulated predation by cod and the starvation.

Migration

Movement of the super-individuals was performed using a simple model based on direction, velocity, and temperature boundaries (Table 1). Swimming was assumed to have directed d_X and d_Y and stochastic components s_x and s_y along the x and y axes. Current vectors were added to the swimming to generate the net displacement of super-individuals. The directed movement was generated from the directions and relative velocities listed in Table 1. The subscripts w and m refer to immature and mature (capelin only) individuals, respectively, in winter and s refers to summer. Temperature has previously been shown to be important in determining the distribution of capelin (Ozhigin and Luka, 1985). Some previous observations (e.g. Anon, 1974; Hamre and Monstad, 1980) suggest that the capelin align their horizontal distribution with temperature fronts in the upper waters. Summer and winter temperatures were therefore implemented in the migration model. TL_w gives the temperature below which the directed winter movement of capelin (DL_w and VL_w) is induced. Similarly TL_m gives the temperature below which the directed movement of pre-spawning capelin (Figure 2, DL_m) is induced. If directed movement is not induced (temperature $> TL_w$) during winter, only the stochastic movement and advection is used to calculate the new position of a super-individual. TL_s gives the temperature below which the capelin is not allowed to move during summer. Also, capelin was not allowed to enter the shallow banks in the Barents Sea, such as the Skolpen bank in the southern part of the Sea, based on observations that the capelin tends to avoid such areas (e.g. Dommasnes *et al.*, 1974). For cod, movement during winter was determined by DC_w and VC_w, while during summer movement was governed by DC_s and VC_s. Cod movement was constrained by a lower temperature limit throughout the year (TC_l), which induces southwards movement and an upper temperature limit TC_u which induces northwards movement. Since the horizontal position of temperature fronts may vary with depth, the temperatures at 50 and 200 m

Table 1. Specification of the movement criteria used in different simulations. The subscripts w and m refer to immature and mature individuals, respectively, in winter, and s in summer. DL, VL, and TL refer to movement direction, relative swimming velocity, and temperature thresholds (°C), respectively, of capelin. DC, VC, and TC refer to movement direction, relative swimming velocity, and temperature thresholds (°C), respectively, of cod. S is south, SW is southwest, SSW is south-southwest, WSW is west-southwest, N is north, NW is northwest, NNW is north-northwest, NNE is north-northeast.

	Capelin								Cod					
Sim	DL_w	DL_s	VL_w	VL_s	TL_w	TL_s	DL_m	TL_m	DC_w	DC_s	VC_w	VC_s	TC_l	TC_u
1	S	NNE	0.8	0.4	3.0	0.0	SW	3.5	S	NNE	0.10	0.05	0.0	7
2	SSW	NNW	1.0	0.2	2.0	−0.5	SSW	4.0	SSW	NNW	0.05	0.10	0.5	8
3	WSW	N	0.7	0.1	2.5	−1.0	SW	3.0	SW	N	0.05	0.15	2.0	9
4	SW	N	1.0	0.2	2.5	−1.5	SSW	4.0	SW	N	0.05	0.10	1.0	9
5	SW	NNE	0.9	0.1	2.5	−0.5	S	4.5	S	N	0.10	0.10	1.0	10
6	S	N	1.0	0.3	3.0	−1.5	S	5.0	SSW	N	0.15	0.15	1.0	10
7	SW	NNW	1.0	0.2	3.5	0.0	S	4.0	SSW	NW	0.05	0.05	1.5	9
8	SSW	N	0.8	0.2	2.5	0.5	SSW	4.5	SSW	NNE	0.10	0.10	1.5	9
9	SW	NE	0.9	0.1	3.0	−0.5	S	4.0	S	NNE	0.15	0.10	0.5	10
10	SW	N	0.6	0.1	2.5	−1.5	SW	4.0	SSW	NNW	0.05	0.05	1.0	8
11	S	NNW	1.0	0.2	2.5	−2.0	SSW	3.5	SW	NNW	0.05	0.15	1.0	7
12	SSW	N	1.0	0.2	3.0	−1.0	SSW	4.0	S	N	0.10	0.20	2.0	9
13	SW	N	1.0	0.3	3.0	−1.5	SW	3.5	S	N	0.05	0.05	3.0	10
14	SW	NNE	1.0	0.3	2.5	−1.0	SSW	4.0	SSW	N	0.10	0.03	1.5	9
15	SSW	N	1.0	0.2	2.5	−1.5	S	4.0	SW	N	0.05	0.15	1.0	9

rather than average temperatures in the water column were used in the movement models of capelin and cod, respectively.

Both directed (d_X, d_Y) and stochastic (s_x, s_y) movement have a range of [−0.5,0.5], and relative displacement thus is in the range [−1,1]. During the spawning migration, when movement is highly directional, the stochastic component was left out, and instead d_x and d_y had the range [−1,1]. The relative displacement was multiplied by the maximum daily swimming distance D_{max} to yield the displacement in each direction (M_X and M_Y):

$$M_X = (d_X + s_x) \times D_{max} \tag{7a}$$

$$M_Y = (d_Y + s_y) \times D_{max} \tag{7b}$$

D_{max} was calculated as the distance swum at maximum swimming speed over a day. Cod was always assumed to have a maximum swimming speed of one body length (bdl) s^{-1}. Capelin generally also had a maximum swimming speed of 1 bdl s^{-1}, but during the spawning season the maximum swimming speed was set to 3 bdl s^{-1} (Hafsteinsson and Misund, 1995). The movement distance was then calculated as:

$$D_{tot} = \sqrt{M_X^2 + M_Y^2} \tag{8}$$

If $D_{tot} > D_{max}$, the movement vector was corrected accordingly by D_{max}/D_{tot}. After the distance swum by the fish had been calculated, the current vectors (C_X and C_Y) generated by the ocean circulation model were added:

$$\Delta X = M_X + C_X \tag{9a}$$

$$\Delta Y = M_Y + C_Y \tag{9b}$$

where ΔX and ΔY are the net displacements in either direction used to calculate the movement vector. Since the polar-stereographic grid is tilted, a correction was made to get true heavenly directions, and allow implementation of strategies such as ‘‘move south’’.

Capelin was assumed to be mature if longer than 14.2 cm at the start of the simulation (Tjelmeland and Bogstad, 1993). Knife-edge maturation at 75 cm was assumed for cod (Ajiad *et al.*, 1999). Since the spawning migration of cod is relatively well known, this topic was not pursued here. Movement vectors were generated so that the mature part of the population is transported to Lofoten during the spawning season.

Comparing simulations and observations

The study was performed by testing various parameter values in the movement models (Table 1) for capelin and cod, and validating these against observed distributions, weight-at-age, and consumption. The range of movement parameter values tested was selected based on previous experience and test runs of the model; many unreasonable parameter values that, for example, yield northwards movement in winter were left untested. The best movement model as determined from comparing predicted and observed distributions was then used to study the interaction between the species in more detail.

The year was divided into a winter and a summer period (Figure 2). The simulations were initiated on 1 October. Comparisons of predicted and observed spatial distribution are made in February and September, while the proportion of mature capelin reaching the observed spawning ground is determined in April. The combined success of the winter and spawning migrations of mature capelin was calculated as the proportion of mature individuals entering the observed spawning areas during February−April. Predicted and observed abundances were compared using root mean square (RMS) calculated as:

$$\mathrm{RMS} = \sqrt{\frac{1}{S}\sum_{j=1}^{j_{\max}}(P_j - O_j)^2} \qquad (10)$$

where P_j and O_j are the predicted and observed relative fish abundances (proportion of total abundance found in square j), jmax is the total number of squares, and S is the number of squares with observations and/or predictions. This calculation was performed for both species at each of the four comparisons between predicted and observed spatial distributions (Figure 2). Finally, the RMS was summed over the entire study period. The different simulations were evaluated using RMS, and low RMS relative to other simulations indicates better performance. All correlations referred to below are Pearson correlations.

Results

Spatial distribution

There was large variability in the performance of the simulations (Table 2). Simulation 10 had the highest average spatial validation rank, and was used to study the interaction between cod and capelin. This simulation used 2.5°C and 4.0°C as northeast temperature boundaries for immature and mature capelin, respectively, and relied on southwest and northwards migrations during winter and summer, respectively (Tables 1, 2). During summer, the capelin was predicted to stay in water warmer than −1.5°C. The predicted monthly spatial distributions of capelin during 1990−1991, and the corresponding observed distributions, are shown in Figure 3. During this period there was a relatively high capelin biomass, medium to high temperatures, and an average fit between predictions and observations compared with the other years (1990−1991 is ranked 2, 5, 1, 5, and 3, respectively, for the five validation points given in Table 2). During January−February the initial separation between the juvenile and maturing fish is noticeable, with the juveniles generally residing northeast of the maturing fish. In March−April this separation is clear, as the mature fish has migrated all the way to the coast for spawning while the immature capelin remain in the central part of the Barents Sea (Figure 3). The spawning area is indicated in the April map of the observations. Finally, the juvenile fish move towards the north during summer.

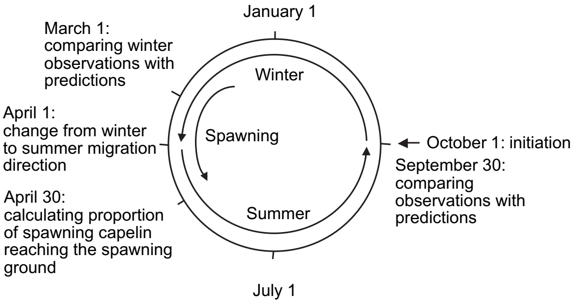

Figure 2. The temporal structure of the study with model initiation in the Fall and comparisons with observed cod and capelin distributions in March, capelin spawning in April, and cod and capelin distributions in September. The arrows indicate the time span for using the winter, summer, and spawning (capelin only) migration directions.

For cod, the NNW direction (Table 1) during summer and SSW direction during winter produced the best fit to observations (Table 2). The lower and upper temperatures for inducing southwards and northwards movement were 1°C and 8°C, respectively (Tables 1, 2). Movement was generally slower than for capelin (Table 1). The predicted monthly spatial distributions of cod during 1990−1991, and the corresponding observed distributions, are shown in Figure 4. From December onwards the spawning migration of the adult stock towards the Lofoten Islands is seen in the lower left corner, while the remaining part of the stock overlaps extensively with capelin. In summer, the cod moves north and is spread over a large area of the Barents Sea.

Growth, mortality, and consumption

Predicted average capelin weight-at-age was in fair agreement with observations (Figure 5a), but was not significantly correlated (O2 vs. P2: $r^2 = 0.34$, $p > 0.05$, O3 vs. P3: $r^2 = 0.22$, $p > 0.05$). The average observed weight for 2-year-old capelin during the study period was 11.7 g, and the corresponding predicted weight was 9.6 g. Capelin weight-at-age was positively correlated with the summer temperature boundary TL_w of different simulations (Table 1, $r^2 = 0.47$).

Cod weight-at-age was predicted with a greater accuracy than for capelin (Figure 5b). The average observed weight of 6-year-old cod during the study period was 2968.7 g, and the corresponding predicted weight was 3414.1 g. Significant correlations between observed and predicted values were found for both 3- and 6-year-olds (O3 vs. P3: $r^2 = 0.91$, $p < 0.01$, O6 vs. P6: $r^2 = 0.69$, $p < 0.05$). Still, there were

Table 2. Comparison of the model predictions against observations. February and September (RMS) refer to the root mean square of predicted−observed distributions, spawning (Proportion) is the proportion of mature capelin reaching the observed spawning area, WL_2 and WC_6 are the predicted average weights (g) for 2-year-old capelin and 6-year-old cod, respectively. Consumption refers to average annual consumption of capelin by cod during 1991−1996. The best overall simulation, based on a non-parametric ranking procedure for the five spatial model-data comparisons, is indicated in boldface numbers.

	Capelin				Cod			
Simulation	February (RMS)	Spawning (Proportion)	September (RMS)	WL_2	February (RMS)	September (RMS)	WC_6	Consumption (Million tonnes)
1	0.0043	0.62	0.0060	7.0	0.00083	0.00065	2 770.6	0.53
2	0.0043	0.53	0.0030	6.7	0.00087	0.00085	3 190.7	0.80
3	0.0033	0.77	0.0017	8.1	0.00095	0.00095	3 257.5	0.85
4	0.0044	0.70	0.0020	10.7	0.00092	0.00090	3 289.5	0.89
5	0.0042	0.63	0.0018	11.4	0.00085	0.00075	3 334.5	0.89
6	0.0054	0.25	0.0027	6.5	0.00103	0.00087	2 693.8	0.44
7	0.0054	0.54	0.0018	34.2	0.00090	0.00087	3 589.5	0.99
8	0.0039	0.54	0.0037	7.2	0.00093	0.00083	3 043.4	0.71
9	0.0042	0.54	0.0016	17.1	0.00093	0.00070	3 377.5	0.86
10	**0.0033**	**0.76**	**0.0017**	**9.5**	**0.00088**	**0.00082**	**3 446.4**	**0.99**
11	0.0052	0.38	0.0019	5.8	0.00093	0.00103	2 863.1	0.56
12	0.0051	0.53	0.0021	10.8	0.00085	0.00087	3 099.0	0.76
13	0.0040	0.75	0.0016	12.6	0.00087	0.00087	3 112.7	0.79
14	0.0043	0.70	0.0029	8.6	0.00093	0.00083	2 986.5	0.70
15	0.0051	0.40	0.0027	9.0	0.00092	0.00093	3 186.3	0.76

some problems; for example in 1992, when weight-at-age was predicted to be much higher than observed. The poor growth in the latter part of the study period following the collapse of the capelin stock was predicted.

Capelin biomass was predicted to vary in a pattern similar to that of the observed biomass data, although there were some discrepancies; for example, in 1992 when the predicted biomass was quite a bit higher than observed (Figure 6). The maximum predicted capelin consumption by cod was about 1.9 million tonnes in 1991−1992 (Figure 6). There was considerable interannual variation in the biomass of capelin consumed by cod (Figure 6), reflecting the variation in capelin biomass. Also there was a pronounced seasonal variation in capelin consumption by cod, with a peak in February−April coinciding with capelin over-wintering and spawning (Figures 3, 4). Capelin consumption by cod was negatively correlated with the directed migration speed of capelin during summer, VL_s (Table 1, $r^2 = 0.54$). Capelin mortality as a result of starvation was predicted to be about 20% per year. In the simulations given in Table 2, cod movement was not made a function of capelin biomass, even though this is likely to be an important factor in motivating cod movement. We therefore tested a simple strategy where cod super-individuals move in a randomly chosen direction if no capelin is encountered. When this strategy is used with parameter values from simulation 10 when capelin is present, the consumption estimate is increased by 30% (Figure 6), and the cod distribution becomes much more aggregated than shown in Figure 4.

Model sensitivity to predation parameters

The parameter setting for the half saturation constant of cod was a bit uncertain. When the KC parameter (Equation 5) was decreased by one order of magnitude there was a 25% increase in average capelin consumption by cod; when it was increased by one order of magnitude the consumption was decreased by 50% relative to the consumption estimate predicted by simulation 10. Average capelin consumption in each of the simulations was strongly correlated to cod weight-at-age ($r^2 = 0.92$, for 6-year-old cod). Changing the ration of other food given to cod had a relatively minor impact on capelin consumption. When OF was doubled from 0.2 to 0.4, the consumption of capelin was increased by 8%. At a zero ration of other food (OF = 0), the consumption was decreased by 14%. This was due to the increased growth of cod with increased consumption of other prey, which again increases the consumption of capelin, since no prey selection was included in the model.

Discussion

We have presented a novel approach for studying interactions between migratory fish populations based on simulating the movement and predator−prey interactions using IBM. This modelling approach is flexible and allows many aspects of real fish populations to be implemented. Here we have used a process-based model structure with a high level of realism and compared the model directly against observations. Thus, the ambition is to develop

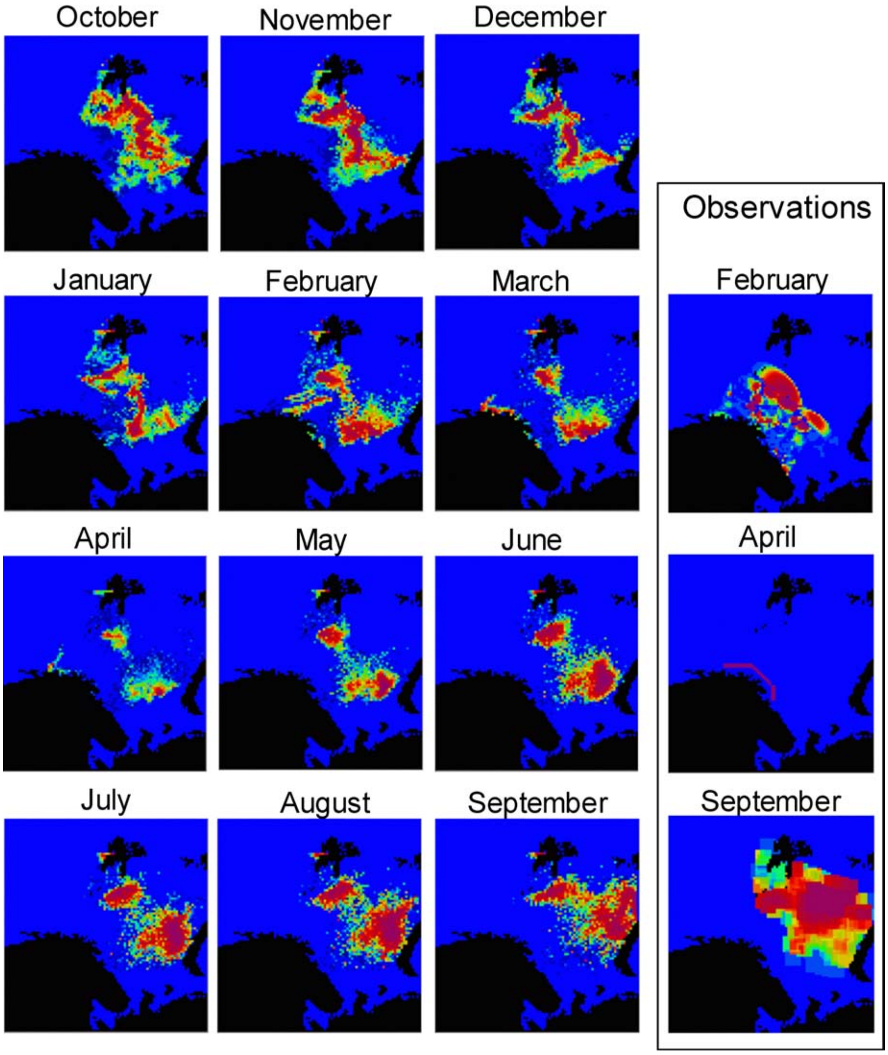

Figure 3. Predicted spatial distribution of capelin from October 1990 to September 1991 using simulation 10. Observed spatial distributions of capelin for February and September are shown to the right. The observed spawning area in 1991 is inside the purple fields for the April panel, but no acoustic observations for the remaining part of the stock are made at that time. The colour indicates relative capelin density (red indicates high density).

a modelling approach that can be used to study interactions between fish populations as well as contribute to fisheries management. Even though there are some discrepancies between predictions and observations, the results obtained here with regard to spatial distribution, growth, and consumption are promising.

The model captured the pattern in interannual growth of cod fairly well, with relatively high growth during the first part of the period, and lower growth towards the end of the period following the collapse of the capelin stock in 1993−1994. The present implementation of ‘‘other food’’ for cod was simplistic. Using a conditional expression for other food, dependent on the availability of capelin instead of a fixed proportion as used here, would probably have improved the predicted weight-at-age for cod. Cod becomes increasingly more piscivorous with increasing body size (Mehl, 1989), and adding such ontogenetic changes in diet would probably have improved the fit of predicted weight-at-age with observations. Cod’s consumption of capelin was predicted to be lower than previous estimates based on stomach content analysis (Figure 6; Bogstad *et al.*, 2000; Dolgov, 2002). However, there was a high correlation between the present and the previous annual consumption estimates. For example, the correlation coefficients between the consumption estimated by Bogstad *et al.* (2000) and the present estimates were 0.92 and 0.94 for predictions I and II, respectively (Figure 6). These correlations are higher than the correlation between the

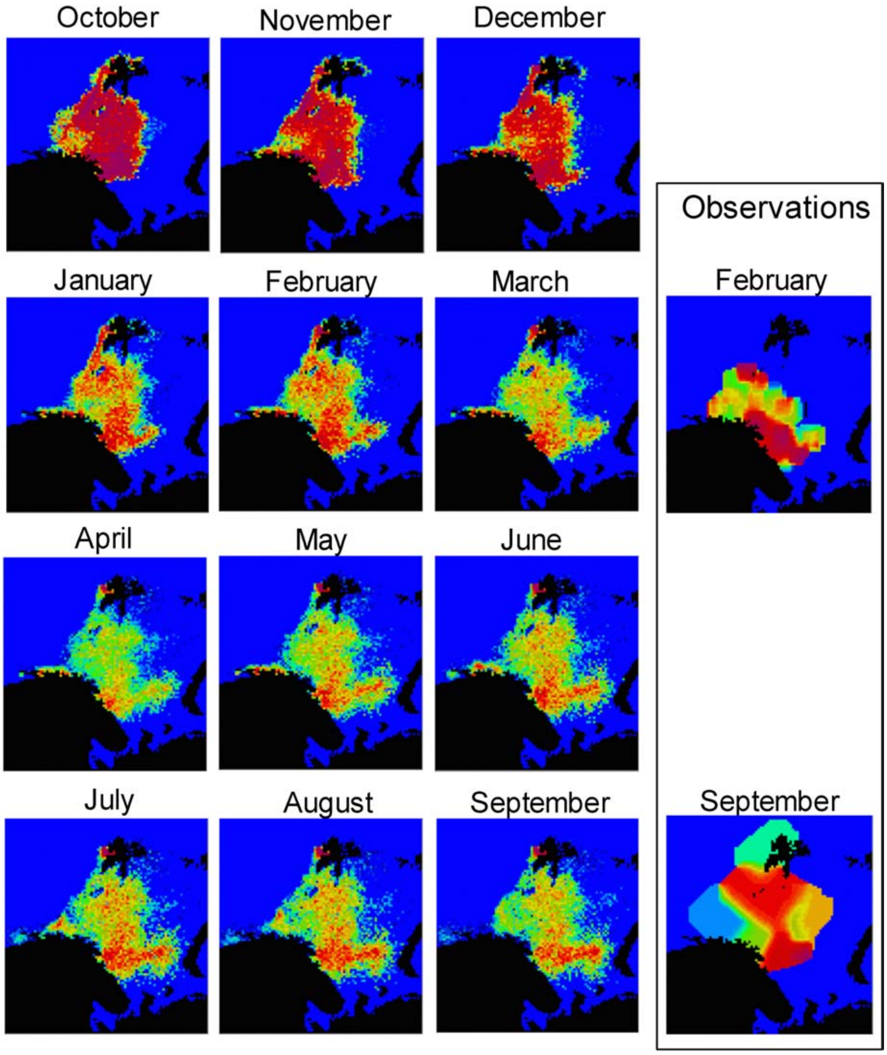

Figure 4. Predicted spatial distribution of cod from October 1990 to September 1991 using simulation 10. Observed spatial distributions of cod for February and September are shown to the right. The colour indicates relative cod density (red indicates high density).

consumption estimates reported by Bogstad *et al.* and Dolgov ($r^2 = 0.85$), which are based on the same stomach content database. Given that the present model is made from first principles, simulating the actual interaction between the two populations, the predicted fit to the previous consumption estimates is good. It is also notable that the best movement model (simulation 10) produced the highest consumption estimate (Table 2), which means that this estimate was closest to the estimates obtained by Bogstad *et al.* and Dolgov. This reflects the importance of including the degree of spatial overlap in predator−prey models. The simple rule that cod will move in a randomly chosen direction if no capelin is encountered increased cod consumption of capelin by 30% and changed the spatial distribution of cod markedly. The capelin, too, is likely to respond to cod density (Fiksen *et al.*, 1995), so that movement models for both predator and prey behaviour need to be addressed, as called for in a recent review (Lima, 2002).

Capelin growth is known to vary interannually as a function of climatic conditions (Gjøsæter and Loeng, 1987; Skjoldal *et al.*, 1992) and density dependency (Hopkins and Nilssen, 1991). In 1991 and 1992, the predicted capelin weight-at-age was similar to the observed values. During 1993, 1994, and 1996 growth was underestimated, while in 1995 it was overestimated. Clearly, there is some interannual variation in capelin growth that is not captured by the model. It is difficult to point to the specific causes of these discrepancies, but most likely they are linked to prey dynamics and/or bioenergetics. The relatively high mortality caused by starvation remains unverified although there can be large seasonal variation in

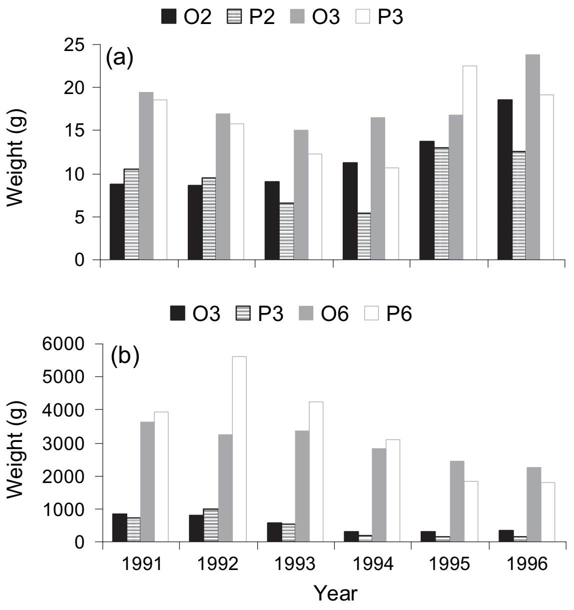

Figure 5. Comparison between observed and predicted weight for 2- (O_2 and P_2) and 3-year-old (O_3 and P_3) capelin (a), and 3-year-old (O_3 and P_3) and 6-year-old (O_6 and P_6) cod (b) at the end of the simulation in September using simulation 10.

condition of capelin (Gjøsæter, 1998). These issues need to be addressed in future studies.

The migration models used here were simple, but still they captured much of the dynamics of capelin and cod migrations. A simple strategy such as move north during the summer half of the year, and southwest during the winter half of the year, linked with temperature information produced fairly good correspondence with observed capelin distributions. It should be noted that the directed movement is subject to advection, such that the net displacement will differ from the directed movement direction. We found that using the temperatures 2.5°C and 4°C at 50 m as a northeast boundary in winter for immature and mature capelin produced the best correspondence between predictions and observations. It is noteworthy that such temperature fronts can recreate important aspects of the spatial dynamics of the capelin stock. This feature is reflected in distribution maps from the 1970s, and therefore seems to be a general aspect of capelin migrations. At the other end of the spectrum, the maximum northern extension of the capelin distribution during summer fitted well with the −1.5°C front at 50 m. In these frontal areas there is usually extensive thermal stratification during Fall, and the capelin tend to migrate vertically between cold, prey rich areas during daytime, and warm waters at night (G. Huse, unpublished data). Sub-zero temperatures are not well suited for growth, but such waters may be rich in prey (Hassel *et al.*, 1991). The thermal stratification complicates the prediction of the position of thermal fronts, and thus the northern extension of the capelin distribution during Fall. Similar relations between temperature and fish distribution have been reported for sockeye salmon as well (Rand, 2002). The model results give a wider distribution of capelin and cod in February than the survey indicates. However, the survey coverage is limited by ice, and parts of both stocks are probably distributed under the ice (north and east of the survey area) at this time of the year. Also, the survey in 1991 did not cover the entire ice-free part of the Barents Sea. Thus, the difference between observed and modelled distributions in February is probably smaller than Figures 3 and 4 indicate.

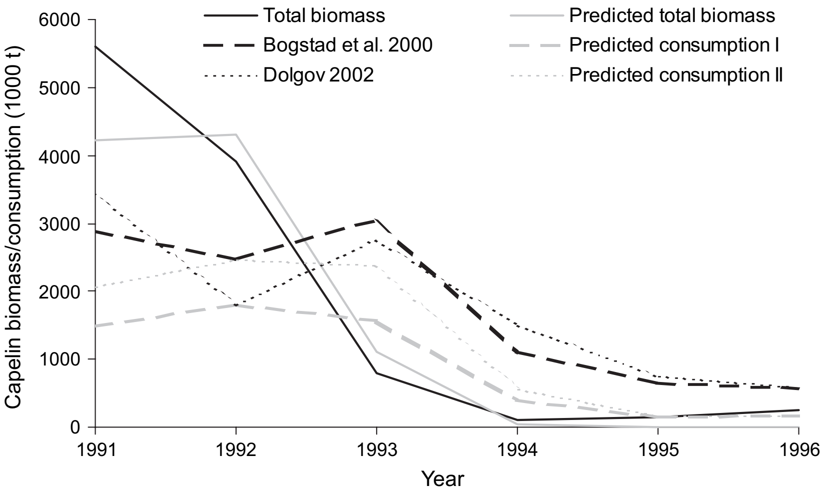

Figure 6. Observed and predicted total capelin biomass, and capelin consumption by cod during 1991–1996. Bogstad *et al.* (2000) and Dolgov (2002) refer to previously reported consumption estimates. Predicted consumption I refers to output from simulation 10, while predicted consumption II refers to a simulation where cod move in a randomly chosen direction if no capelin is present.

The model presented here describes the basic rates of growth, mortality, and consumption of the target stocks, which are essential components of population models including fisheries assessment models. This makes it easy to investigate the effects that various spatial processes have on the model results. At present, spatial dynamics are rarely considered in fisheries assessment models. In ''traditional'' multispecies models where migration is included (e.g. MULTSPEC; Bogstad *et al.*, 1997), it is not process-based. Interannual variation in overlap between cod and capelin during the capelin spawning migration could for example be included in the assessment methodology presently used for capelin (Gjøsæter *et al.*, 2002).

To our knowledge, this is the first attempt to simulate the interaction between two fish populations in a model, which is initiated by observed data on spatial distribution, size, and age, and includes daily movement and a fine scale environment description. Models such as the one presented here can be valuable tools for studying how spatial processes affect the growth, survival, and interaction of fish populations, and may for example be used to address climate change effects on fish stocks and issues related to ecosystem-based management. There is need for further investigation into how different movement rules affect the interactions between the target species and the validity of other assumptions, in particular regarding capelin growth. Rather than seeing this contribution as an end result, it should be viewed as a starting point for future explorations of spatial IBM applied to fish populations where migration is an important part of the stock dynamics.

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