Relevance of cod (*Gadus morhua* L.) predation for inter-cohort variability in mortality of juvenile Norwegian spring-spawning herring (*Clupea harengus* L.)

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Mortality of juvenile Norwegian spring-spawning herring growing up in the Barents Sea is characterized by a high inter-cohort variability. Variable predation pressure from the north-east Arctic cod stock has been proposed as an explanation, but it has been difficult to test this hypothesis with actual field data.

Data on the abundance of the main fish stocks in the Barents Sea ecosystem, collected by the Institute of Marine Research in Bergen during the period 1983–1993, were analysed to test this hypothesis. Since capelin has been the major prey of cod during the period investigated, the relationship between herring juvenile mortality and the abundance of cod, capelin and herring was investigated. More than 90% of the inter-cohort variation in mortality of juvenile herring observed during this period was explained by a simple model using the ratio of capelin abundance to the abundance of juvenile cod as the explanatory variable. The relationship is strong enough to warrant using the simple model for improving the short-term forecasts of recruitment to the spawning stock of Norwegian spring-spawning herring.

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Introduction

Understanding the factors that control recruitment to the adult or exploited stock of marine fish, or year-class strength, is of fundamental importance in fisheries science. Much of the research work on this topic has been centred around Hjort's (1914) starvation hypothesis (Wooster and Bailey, 1989). Despite the conceptual appeal of the theory and a large concentration of efforts, it has not yet been possible to verify the hypothesis from field data (Houde, 1989).

More recently, attention has focused on predation as an important mechanism contributing to the observed changes in recruitment. The widespread occurrence of predation on all pre-recruit stages of fish suggests that this mechanism could be responsible for much of the variability observed in year-class strength (Sissenwine, 1984; Bailey and Houde, 1989; Houde, 1989). Several studies have also shown that mortality due to predation on the late larval and early juvenile stages has the potential to influence recruitment to the adult stock more than mortality occurring during the early larval stages (e.g. Sissenwine, 1984; Smith, 1985; Peterman *et al.*, 1988; Smith *et al.*, 1991; Hartman and Margraf, 1993).

Studies based on analysis of stomach contents (e.g. Daan, 1987; Sparholt, 1990; Bogstad and Mehl, 1992) have shown that the amount of juvenile fish consumed by predators is large enough to explain a substantial part of the variations in year-class strength. Simulation

studies (e.g. Lævastu and Bax, 1991) also demonstrate that predation can potentially regulate year-class strength.

The main difficulty associated with predation studies has been to demonstrate that changes in predation pressure actually affect the net mortality rate of the prey; i.e. to demonstrate that the mortality caused by predators is additive relative to the mortality due to other causes (Sparholt, 1990). If predators consume mostly sick, weak or otherwise ''displaced'' individuals (Jones, 1982) which have a high probability of dying, the effect on the net mortality rate of the prey population of a change in the predator's abundance will be reduced. If, on the contrary, they mostly eat viable individuals, then large changes of predator abundance may have drastic effects on the mortality of the prey stock. This question is difficult to investigate by studies based on analysis of stomach contents alone, since the presence of individuals of one species in the stomach of another does not clearly indicate what the condition of the prey specimen was before it was ingested. Therefore, it is necessary to combine the information from stomach analysis studies with information on abundance and mortality rates of the prey and predator populations to demonstrate that the net mortality rate of the prey populations responds to changes in the predator population in a way consistent with current knowledge and theories on predator–prey interactions (Walters *et al.*, 1986).

The Norwegian spring-spawning herring stock is characterized by a high variability in year-class strength (Hjort, 1914; Dragesund, 1971; Garrod, 1982; Serebryakov, 1991). The Barents Sea is an important nursery area for this stock (Dragesund *et al.*, 1980), and strong year-classes of herring are dominated by fish from this area (Dragesund, 1970; Seliverstova, 1990a,b). Barros and Toresen (1998) have shown that inter-cohort variability in survival of the juvenile part of the stock growing up in the Barents Sea is very high, and that many of the cohorts entering the area are practically extinct by the end of the juvenile period.

The Barents Sea ecosystem is dominated by cod, capelin, and juvenile herring (Hamre, 1988, 1994). Hamre (1988) has hypothesized that most of the variability in mortality of juvenile herring is due to cod predation. According to this hypothesis, increased predation pressure on herring by cod is caused by a decline in the stock of capelin, the preferred prey of cod (Mehl *et al.*, 1986; Mehl and Sunnanå, 1991). The analysis of cod stomach samples collected by the Institute of Marine Research in Bergen (IMR) and the Polar Research Institute of Marine Fisheries and Oceanography in Murmansk (PINRO) since 1984 largely supports this hypothesis (Orlova *et al.*, 1995). As discussed above, however, they alone are not enough to show that this likely increase in consumption caused a higher mortality in the juvenile herring population.

The purpose of this paper is to test the hypothesis that most of the inter-cohort variability in survival of juvenile Norwegian spring-spawning herring in the Barents Sea is due to variable cod predation (Hamre, 1994). We also provide some results which indicate that this hypothesis can be used to build a predictive model for the survival of juvenile herring in the Barents Sea.

Data

Barros and Toresen (1998) have provided estimates of mortality rates of juvenile Norwegian spring-spawning herring in the Barents Sea area for the year-classes 1983–1985 and 1988–1993, using a series of acoustic abundance estimates which included several estimates, at distinct ages, of each cohort that entered the Barents Sea between 1983 and 1993 (cohorts 1983–1985 and 1988–1993). This study is based on those year-classes.

Estimates of mortality and abundance of juvenile herring

Most of the inter-cohort variability in mortality of juvenile herring in the Barents Sea is associated with the first months of the 0-group stage (Barros and Toresen, 1998). The mortality values used in this study should therefore be related to this period, which corresponds roughly to the months between August and October of the year of birth of each cohort.

Barros and Toresen (1998) have estimated juvenile survival curves for the whole juvenile period (ages 0–3 years) of each of the 1983–1985 and 1988–1993 herring cohorts. They have also shown that these nine survival curves could be grouped in two clearly distinct categories, those of the ''low-survival cohorts'', with an expected overall juvenile survival close to 0%, and those of the ''high-survival'' cohorts, with an expected overall juvenile survival in excess of 10–15%. They estimated an expected survival curve for each of these groups. In this paper, as in Barros and Toresen (1998), the description of herring juvenile survival, considering a distinct survival curve for each cohort, will be called the ''full model'', while that using only two summary survival curves will be called the ''two-level survival model''.

To get appropriate estimates of mortality for this study, the survival, S, experienced by each of the herring cohorts investigated from the beginning of August to the end of October of their first year of life was estimated using the full model. Given S, mortality during the period is then $1 - S$. The mortalities computed in this way will reflect most of the inter-cohort variability in this parameter, while still referring to a well-determined period in the life of the herring.

The estimates of 0-group herring abundance used are those estimated for the start of August of the year of

birth of each cohort, using the two-level survival model. Use of model values, rather than observed values, was required because the timing of the acoustic values estimates of 0-group herring available has not been constant for all years. The acoustic estimates for the different cohorts are not, therefore, directly comparable. The two-level survival model is used to estimate these abundances because mortality and abundance estimates are not independent quantities. Therefore, correlation problems could arise if abundances and mortalities were estimated from the same model. Since the mortality estimates were computed under the full model, this approach may reduce the problems associated with the correlation between the mortality and 0-group abundance estimates, while providing estimates of 0-group herring abundance, which are directly comparable across cohorts. The estimates of abundance in numbers provided by this procedure were converted into biomass using the length distributions from the International 0-group surveys (ICES, 1983, 1984, 1985, 1988, 1989, 1990, 1991, 1992, 1993) and the corresponding length–weight relationship.

Cod abundance

A requirement for the estimate of cod abundance used in this study was that it should correspond closely to the expected variations in predation pressure from the cod stock on the 0-group herring.

It is known that not all parts of the cod stock will influence equally the survival of juvenile herring. The first choice to be made, therefore, was which segment(s) of the cod stock should be considered. For this study, it was decided to use the cod age-groups 1 to 3 years.

The choice of these age-groups was based on the following observations:

(a) in August–October, the 0-group herring, transported into the Barents Sea by the dominating currents, will tend to have a greater geographical overlap with the younger cod than with the older specimens (Mehl *et al.*, 1986; Bergstad *et al.*, 1987; ICES, 1994a);

(b) optimal foraging considerations (Kerr, 1971; Stephens and Krebs, 1986) and observations of stomach contents (Wiborg, 1960; Ponomarenko, 1983; Orlova, 1992; Bogstad *et al.*, 1994; Orlova *et al.*, 1995) suggest that cod preying on fish will tend to eat the largest prey they can catch and handle, and that cod can already eat fish prey of up to 50% of their own size when in the 0-group stage. In August–October, 0-group herring range from 5 to 12 cm in length (ICES, 1983, 1984, 1985, 1988, 1989, 1990, 1991, 1992, 1993), and are therefore in the ideal size-range for cod between 20 and 40–50 cm (corresponding approximately to age-groups 1 to 3 years in August–October – Mehl and Nakken, 1994);

(c) if the large changes in herring mortality are due to variable cod predation, then the part of the cod stock responsible for these changes should also show relatively large variations. The largest oscillations in cod abundance are those of the youngest age-groups (Fig. 1), and it is therefore most likely that predation by these age-groups will be responsible for variations in mortality of 0-group herring.

The second choice is which estimates of the abundance of these age-groups should be used. Three different data series on the abundance of cod are available: Virtual Population Analysis (VPA) estimates of stock numbers at age on 1 January; acoustic abundance indices at age from the Norwegian demersal fish surveys in February; and bottom trawl abundance indices from the same surveys. These are indications that mortality of the youngest age-groups of cod may have varied markedly during this period (Korzhev and Tretyak, 1992; Bogstad *et al.*, 1994), therefore VPA estimates, which are based on the assumption of constant natural mortality, should not be preferred if other estimates are available. The acoustic survey index, on the other hand, is hampered by large changes in methodology along the time-series, which make the comparison of the estimates for the different years difficult. Finally, the bottom trawl series index was also affected by the changes in methodology, but to a lesser extent than the acoustic estimates (Aglen and Nakken, 1994). It was therefore decided to use the bottom trawl abundance indices for cod in age-groups 2 to 4 in February, reported by Aglen and Nakken (1994). These indices were back-calculated to mid-September of the year prior to the surveys (corresponding then to age-groups 1 and 3 years), using a constant mortality rate $M=0.2$ for all age-groups between September and February. This will not compensate for the variable mortality among cohorts, but will at least provide a minimal rescaling of the estimates to compensate for the time-lag between the period for which the herring mortalities are calculated and the time of the demersal fish surveys.

Capelin abundance

For the measure of capelin abundance, the estimates of total capelin biomass from the acoustic capelin surveys in September (ICES, 1994b) were used. During August–September, mostly immature capelin will be available for cod (Mehl *et al.*, 1986) but part of the mature capelin may become available by the end of this period, and may influence the predation pressure the cod stocks exert on the juvenile herring.

Data analysis

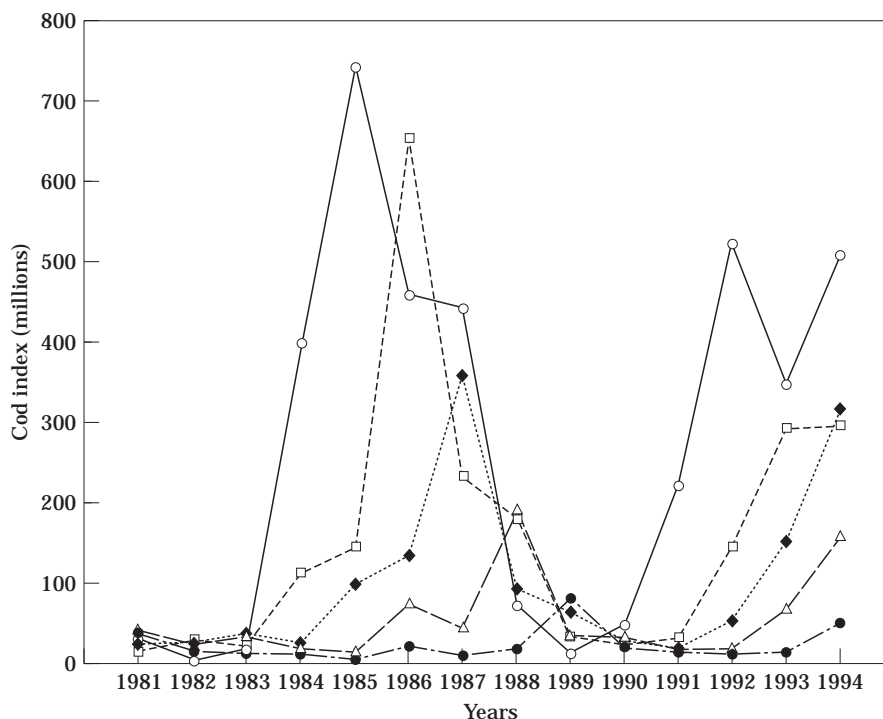Figure 2 (a)–(c) illustrates the variation of herring mortality and the corresponding abundance estimates of

Figure 1. Variability in the abundance of the different age-groups of juvenile north-east Arctic cod in the Barents Sea, as reflected in the trawl abundance indices from the surveys in February during the period 1981–1994. Data from Aglen and Nakken (1994). Age 2 (○); age 3 (□); age 4 (◆); age 5 (△); age 6 (●).

cod, capelin and 0-group herring. Mortalities were high when the cod stock was at a high level, and the capelin stock at a low level, lending some support to the hypothesis of a cause–effect relationship between cod predation and herring mortality.

Figure 3(a)–(b) shows, however, that this relationship is not very well-defined, as there is at least one very high mortality at a very low cod stock level, and a low mortality at high capelin stock levels. Thus, even a low cod stock may generate a high mortality, and high levels of the cod stock do not always generate high mortalities. No relationship between mortality and herring 0-group abundance is apparent from the plot in Figure 3(c).

Several studies (e.g. Lilly, 1987, 1991; Methven and Piatt, 1989; Steinarsson and Stefánsson, 1991; Jørgensen, 1992) have documented that cod has a particular preference for capelin, and that it normally does not manage to replace capelin as its main food source when this prey is not available. Observations from surveys carried out by IMR in the Barents Sea show that 0-group herring is normally distributed very high in the water column, and that, even at this early age, they show strong schooling behaviour, actively avoiding the ship and the trawl. Capelin, on the other hand, are normally found deeper, and show less marked avoidance reactions (J. Hamre, IMR, pers. comm.). If one also considers that the energy content of 0-group herring is lower than that

of capelin (Ajiad *et al.*, 1994), cost–benefit considerations (Stephens and Krebs, 1986) indicate that cod should show a marked preference for capelin, and should only prey intensively on herring (thereby causing a detectable increase in herring mortality rates) when the amount of capelin available is below what would be necessary to cover its food requirements. If the reasoning above is correct and the ratio between the capelin and cod indices is an index of the availability of capelin as food for cod, one will expect herring mortality to vary inversely with this ratio. Figure 4 illustrates that this effect is indeed clear in the data. Even though only a few data points are available, their distribution pattern agrees with the expectations.

To evaluate the strength of this relationship, a statistical model can be fitted to the data. When doing this, one must take into account that not all herring die because of cod predation. Even if there were no cod, or if there were an infinite amount of capelin, a certain proportion of the 0-group herring would still die. If the lowest mortalities observed in the data set can be taken as an estimate of the mortality due to ''other causes'', the mortality of 0-group herring, Y, can be modelled as

$$Y = Y_0 + (1 - Y_0)\frac{e^{\beta_0 + \beta_1 x_1}}{1 + e^{\beta_0 + \beta_1 x_1}} \tag{1}$$
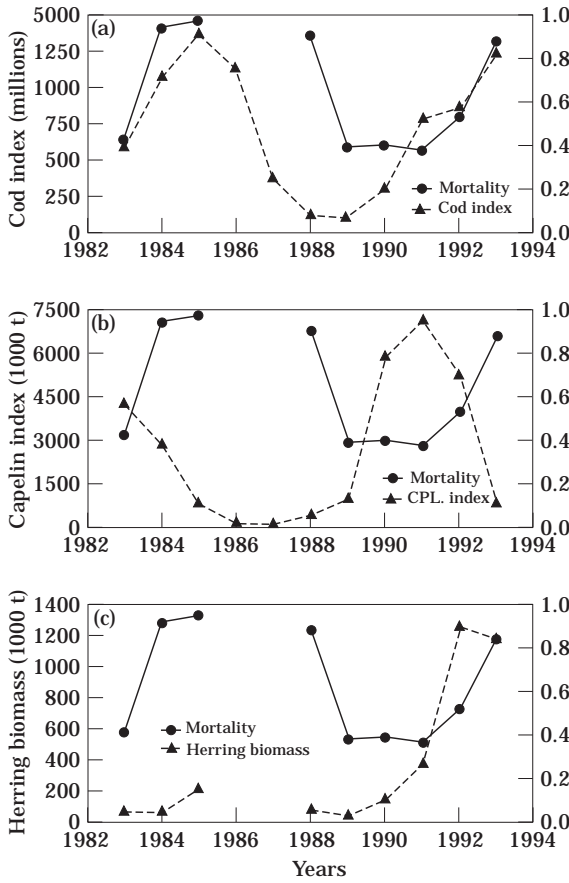
Figure 2. Comparison between mortality of 0-group herring during the months of August through October estimated for the cohorts 1983–1985 and 1988–1993, and the indices of abundance of cod, capelin and 0-group herring for the same period. Herring abundance and mortality estimates were calculated from the models derived by Barros and Toresen (1998). Cod index is the sum of abundance indices for cod aged 2–4 years from Aglen and Nakken (1994), back-calculated to mid-September. Capelin index is total capelin biomass from the annual capelin acoustic surveys (ICES, 1994b).
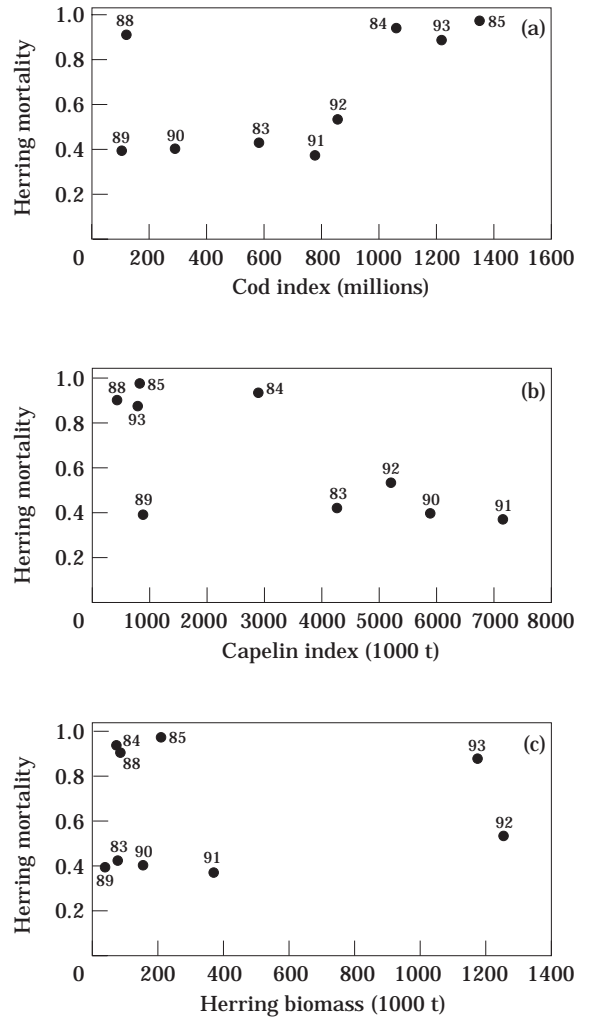

Figure 3. Relationship between the mortality of 0-group herring during the months of August through October for the cohorts 1983–1985 and 1988–1993, and the indices of abundance of (a) cod, (b) capelin and (c) 0-group herring for the same period. Herring abundance and mortality estimates were calculated from the models derived by Barros and Toresen (1998). Cod index is the sum of abundance indices for cod aged 2–4 years from Aglen and Nakken (1994), back-calculated to September. Capelin index is total capelin biomass from the annual capelin acoustic surveys (ICES, 1994b).

where Y_0 is the mortality due to "other causes", X_1 is the capelin/cod ratio, and β_0 and β_1 are the parameters of the model, which can be estimated by ordinary least-squares.

This model gave a good fit to the data (Fig. 4), explaining approximately 97% of the variation in the mortality data. Not surprisingly, the analysis of variance (Table 1) indicates that the fit is highly significant. The significance level of the F-test was determined by randomization (Edgington, 1987). It is not reasonable, however, to assume that herring mortality will depend only on the capelin/cod ratio. This would mean that, in case of a total absence of capelin, a very small cod stock would still cause a 100% mortality on the herring, irrespective of herring abundance. Since this is obviously

not possible, mortality should also depend on the ratio between the abundances of herring and cod. To investigate whether this dependency was detectable in the data set analysed, the ratio between the estimated herring biomass and the cod index was calculated, and a term for this ratio was added to Model (1), which could then be expressed as

$$Y = Y_0 + (1 - Y_0) \frac{e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2}}{1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2}} \qquad (2)$$

$$Y = 0.3713 + (1 - 0.3713)\ \frac{e^{4.766 - 0.978\,X_1}}{1 + e^{4.766 - 0.978\,X_1}}$$
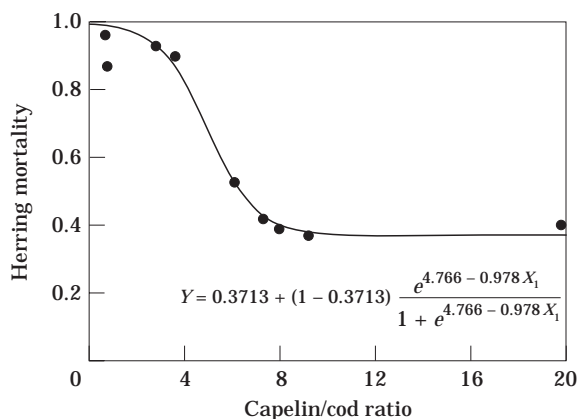
Figure 4. Logistic model fitted to the data on the estimates of mortality of 0-group herring during the months of August through October for the cohorts 1983–1985 and 1988–1993. Independent variable in the model is the ratio between the indices of total capelin biomass and cod numbers (age-groups 1 to 3 years) in September.

where all the terms are the same as in Model (1), X_2 is the herring/cod ratio and β_2 is the corresponding coefficient.

This model was fitted to the same data, and the improvement in the fit of the model achieved by including this extra variable was evaluated by an extra-sum-of-squares analysis (Draper and Smith, 1981). The improvement in model fit achieved by including this term is non-significant (Table 2). It was therefore concluded that this effect cannot be demonstrated for the data available, and Model (1) was accepted as the best

description of these data. To evaluate the importance of the smallest cod for explaining the variability in herring mortality, the capelin/cod ratio was re-calculated using two different measures for the abundance of juvenile cod: first, the number of cod aged 4 and 5 years was added to that of the three age-groups already considered. Next, the calculations were made using only cod in age-groups 2 to 5 years.

The estimated herring 0-group mortalities are plotted against these two quantities in Figure 5(a)–(b). The addition of the two older age-groups introduced a little more noise in the relationship, but did not change it fundamentally. Removal of the 1-group cod, however, resulted in the elimination of the clear separation between the high- and low-mortality cohorts. Fitting Model (1) to these modified data indicates that the inclusion of the older age-groups does not affect the utility of the model very much, as the percentage of variation explained by the model is still above 90% (Table 3).

Removing the 1-group cod, however, reduces this percentage to 60% (Table 4). It is therefore concluded that an important part of the inter-cohort variability in mortality of 0-group herring is associated with predation from the 1-group cod.

Evaluation of the predictive capabilities of the procedure

The abundance of the Norwegian spring-spawning herring stock depends strongly on the more or less periodic appearance of strong or very strong year-classes

Table 1. Analysis of variance table for the fit of Model (1) to the data on mortality of 0-group herring. Variables in model: ratio total capelin biomass/numbers of cod ages 1–3.

Source	Degrees of freedom	Sum of squares (SS)	Mean squares	F-ratio	p-value
Model	1	0.544208	0.544208	222.933	0.002
Error	7	0.017088	0.002441		
Total	8	0.561296	0.070162		

Table 2. Extra sum of squares analysis table comparing the fit of the models with and without the herring/cod ratio term. Model (2) (full model) includes both the capelin/cod and the herring/cod ratios; Model (1) (reduced model) includes only the capelin/cod ratio.

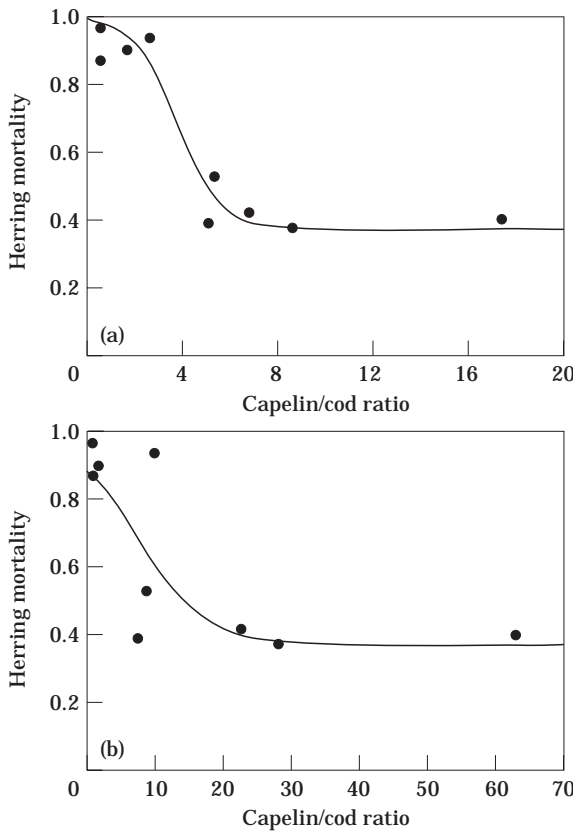| Source	Degrees of freedom	Extra sum of squares (ESS)	Extra mean square (EMS)	F-ratio	p-value
Constant	2	0.544213	0.272107	95.57657	<0.001
Model (1)	1	0.000005	0.000005	0.00176	>0.1
Model (2)	6	0.017083	0.002847		

Figure 5. Logistic model fitted to the data on the estimates of mortality of 0-group herring during the months of August through October for the cohorts 1983–1985 and 1988–1993, using as independent variable two alternative measures of the capelin/cod ratio: (a) ratio between the indices of total capelin biomass and cod numbers (age-groups 1 to 5 years) in September; (b) ratio between the indices of total capelin biomass and cod numbers (age-groups 2 to 5 years) in September.

(Serebryakov, 1991). These year-classes occur only when a large proportion of the juveniles are distributed in the Barents Sea. For this reason, cohorts suffering a "high" mortality in the Barents Sea are not likely to provide one of these recruitment pulses, even if they are very abundant at the start of the 0-group stage.

For medium- and long-term management of this stock, it is of interest to be able to evaluate if there are survival conditions in the Barents Sea for the production of a strong cohort, in case other conditions are favourable. It is therefore of interest to evaluate whether the relationship between herring mortality and capelin and cod abundance can be used to predict the level of mortality expected for the incoming herring year-classes.

Barros and Toresen (1998) could only prove unequivocally the existence of two different survival levels in this data set. It was therefore considered that it would be inappropriate to give predictions of mortality at a higher level of precision. The different cohorts were grouped into two categories, "high-survival" and "low-survival" (Barros and Toresen, 1998). Survival through the juvenile period for cohorts subjected to the low survival regimen will be practically zero, while for the other cohorts it can reach 25%. Predicting mortality for a given cohort may then be reduced to predicting the probability that this particular cohort will belong to the "high-survival" group. One then wishes to evaluate whether this probability can be predicted from the estimates of abundance for capelin and cod provided by the regular resource surveys, and what precision can be attached to such a prediction.

If one represents the high and low survival as 1 and 0, respectively, the probability that cohort **i** will experience a high survival can be related to the capelin/cod ratio by the logistic model (McCullagh and Nelder, 1989)

$$P(Y_i = 1) = \frac{e^{\beta_0 + \beta_1 x_1}}{1 + e^{\beta_0 + \beta_1 x_1}} \tag{3}$$

similar to Model (1) used above, where Y_i denotes a high survival event and the other terms have the same meaning as in Model (1).

Fitting this model to the data on the classification of the different cohorts as high or low survival given by Barros and Toresen (1998) gives a perfect fit, as expected (Fig. 6). For this application, however, the interest lies in evaluating how well this model can predict the probability of a new cohort experiencing a high survival. For this, a cross-validation procedure (Draper and Smith, 1981) was used. One cohort is removed from the data set. Model (3) is fitted to the data from the remaining cohorts, and the parameters estimated from this fitting are used, together with the estimates of the capelin/cod

Table 3. Analysis of variance table for the fit of Model (1) to the data on mortality of 0-group herring. Variables in model: ratio total capelin biomass/numbers of cod ages 1–5.

Source	Degrees of freedom	Sum of squares (SS)	Mean square	F-ratio	p-value
Model	1	0.526545	0.526545	106.0639	<0.001
Error	7	0.034751	0.004964		
Total	8	0.561296	0.070162		

Table 4. Analysis of variance table for the fit of Model (1) to the data on mortality of 0-group herring. Variables in model: ratio total capelin biomass/numbers of cod ages 2–5.

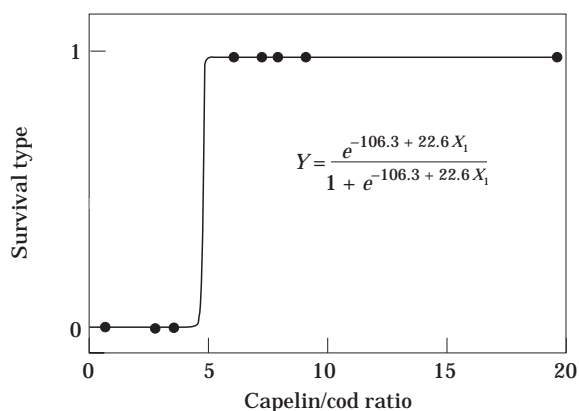| Source	Degrees of freedom	Sum of squares (SS)	Mean square	F-ratio	p-value
Model	1	0.345477	0.345477	11.20538	>0.01
Error	7	0.215819	0.030831		
Total	8	0.561296	0.070162		

Figure 6. Logistic model fitted to the data on the type of survival (high or low survival) for each of the 1983–1985 and 1988–1993 herring cohorts. Independent variable in the model is the ratio (total capelin biomass)/(cod numbers age-groups 1 to 3 years) in September of the same year.

$$Y = \frac{e^{-106.3 + 22.6 X_1}}{1 + e^{-106.3 + 22.6 X_1}}$$

Table 5. Observed outcomes of survival events and cross-validation predicted probabilities of ''high'' juvenile survival for each of the 1983–1985 and 1988–1993 cohorts.

Cohort	Outcome (survival type)	Predicted probability of high survival
1983	High survival	1.00
1984	Low survival	0.00
1985	Low survival	0.00
1988	Low survival	0.00
1989	High survival	1.00
1990	High survival	1.00
1991	High survival	1.00
1992	High survival	1.00
1993	Low survival	0.00

ratio corresponding to the excluded cohort, to predict the probability that this particular cohort will experience a high survival. This procedure is repeated each time excluding a different cohort, until all cohorts have been excluded. The reliability of the procedure is evaluated from the distribution of the differences between the observed outcomes and the probabilities of ''high survival'' predicted from the model.

This probability was above 0.995 for all cohorts classified in the ''high survival'' group, and below 0.005 for all those in the ''low-survival'' group (Table 5). For the period studied (1983–1993), therefore, knowledge of the capelin/cod ratio for a given year was enough to reliably predict the juvenile survival of a herring cohort entering the Barents Sea as 0-group.

Discussion

The results of this study support the hypothesis that cod predation is the main factor influencing variation in the mortality of juvenile herring in the Barents Sea (Hamre, 1994). The effect of the juvenile cod stock on the mortality estimated for 0-group herring is relatively reduced in years when there are large amounts of capelin available, but increases dramatically in years when the relative amount of capelin available to the juvenile cod gets below a given threshold.

Hamre's hypothesis is a particular aspect of the more general hypothesis that variable predation during the juvenile stages may contribute significantly to the determination of year-class strength (Sissenwine, 1984). Thus, this study also supports the latter hypothesis.

The general patterns in the inter-cohort mortality are in relatively good agreement with those arising from the analysis of the cod stomachs (Orlova *et al.*, 1995; B. Bogstad, IMR, pers. comm.). The very large influence of the very young age-groups of cod on the mortality of 0-group herring, however, is a particular aspect which has not yet been specifically addressed within the multi-species research being carried out in the Barents Sea. This effect is nevertheless already partially apparent in the cod stomach data reported by Orlova *et al.* (1995). These data show that in some areas and seasons 1-group cod may have consumed significant amounts of 0-group herring, and that there is a general trend for smaller herring to be found in the stomachs of smaller cod. The observations by Orlova (1992), stating that cod smaller than 50 cm fed on herring between 35% and 52% of their own length indicates also that the 20 cm (1-group) cod should be expected to prey intensively on the 5–12 cm 0-group herring. However, the amount of young herring observed in the stomachs of cod aged 1 year registered in the PINRO-IMR stomach database (Mehl and

Table 6. Average length of 0-group herring sampled during the International 0-group fish surveys in August, 1983–1985 and 1988–1993, and (approximate) average length of 1-group cod in the same period. The cod lengths were calculated by assuming that approximately 2/3 of the yearly growth of the young cod is achieved between February and August (Jørgensen, 1992), and using the average length data in the samples from the demersal fish surveys in February (Mehl and Nakken, 1994).

Year	83	84	85	88	89	90	91	92	93
Herringlength(cm)	8.3	8.4	9.0	6.7	7.9	8.9	7.9	9.0	7.5
Codlength(cm)	22.3	20.3	19.9	22.0	23.6	23.2	21.1	18.3	16.1

Yaragina, 1992) is very low. The most likely explanation for this discrepancy lies in the cod stomach sampling procedure used until recently. It has been shown (Engås and Godø, 1989; Godø and Sunnannå, 1992; Aglen and Nakken, 1994) that the bottom trawl used to sample the cod included in the stomach studies is strongly size-selective, and that more than 70% of the 1-group cod in the path of the gear evaded capture. This is directly reflected by the small number of 1-group cod in the stomach database. Even though this age-group is the most abundant of each cohort, it only represents approximately 5% of the stomachs available in the PINRO-IMR database. In addition, it has been observed (Mehl and Nakken, 1994) that a large proportion of the cod aged 1 and 2 years are distributed pelagically in February, and are not available to the bottom gear. Since 0-group herring are usually distributed in the upper 50 m of the water column (ICES, 1994a), any cod preying on them must also be distributed pelagically. As only a small fraction of these fish are available to the bottom trawl (Mehl and Nakken, 1994), the probability that they will be included in the stomach samples taken by the latter gear must be considered to be quite low. Routine pelagic trawling for cod has recently been included in the IMR survey procedures (Mehl and Nakken, 1994), and it is thus likely that enough data to investigate this problem will soon be available.

The association between the mortality of herring and the relative abundance of capelin, which is a fundamental element in Hamre's (1988, 1994) hypothesis, is very clear in the analysis, and can also be detected from the analysis of cod stomachs, as is evidenced by the work of Orlova *et al.* (1995). This aspect of the results from the stomach studies is not rigorously quantified, however, and more observations will be needed, from areas and periods when the small cod and the herring overlap, before the generality of the observations can be confirmed. The size-dependency of predation implies that using the numbers-at-age as a measure of the cod stock corresponds to the implicit assumption that the size-at-age of the cod and the herring is constant. The sizes of both the 0-group herring and the different age-groups of cod have, however, varied appreciably during the years

studied here (ICES, 1983, 1984, 1985, 1988, 1989, 1990, 1991, 1992, 1993; Mehl and Sunnanå, 1991; Aglen and Nakken, 1994; Table 6).

The variations in herring length are large enough to be reflected in the swimming speed and schooling behaviour of the herring, and may therefore affect the success of cod feeding on them (Pitcher, 1993). The changes in the size of the 1-group cod, on the other hand, imply that it is likely that in some years only a small fraction of this age-group was large enough to prey on the herring, while in other years most of the individuals in the 1-group stage would have been able to consume this prey. The effective number of predators may therefore have varied in a slightly different way from the potential number of predators represented by the simple sum of the numbers-at-age. This effect cannot be evaluated directly from the data available, however, and more studies addressing the size-selectivity problem in predation of herring by cod will be required before it is possible to determine its importance.

The abundance of herring relative to that of the cod could not be shown to have an effect on the mortality of 0-group herring. The most likely explanation for this is that the range of values for this ratio is not sufficiently wide.

Figure 7(a)–(d) represents Model (2), where β_0 and β_1 take the values estimated from the data, while β_2 was given arbitrary values of $\beta_2 = \beta_1$, $\beta_2 = \beta_1/2$, $\beta_2 = \beta_1/3$ and $\beta_2 = \beta_1/4$ respectively. This parametrization reflects the assumption that the value of the herring/cod ratio will only affect the mortality of 0-group herring when the predation pressure by the cod on the herring is significant, that is, when the capelin/cod ratio is low. The relative abundance of herring must be relatively high, however, for mortality to be noticeably reduced. Since the highest observed value of the herring/cod ratio does not exceed 1.5, it must be concluded that this effect cannot be estimated from the data available.

Most papers published on the biological interactions in the Barents Sea (e.g. Mehl *et al.*, 1986; Orlova *et al.*, 1995) stress the importance of considering the changes in geographical distribution of the different stocks, and particularly the overlap between them. The analysis presented in this paper did not consider explicitly the
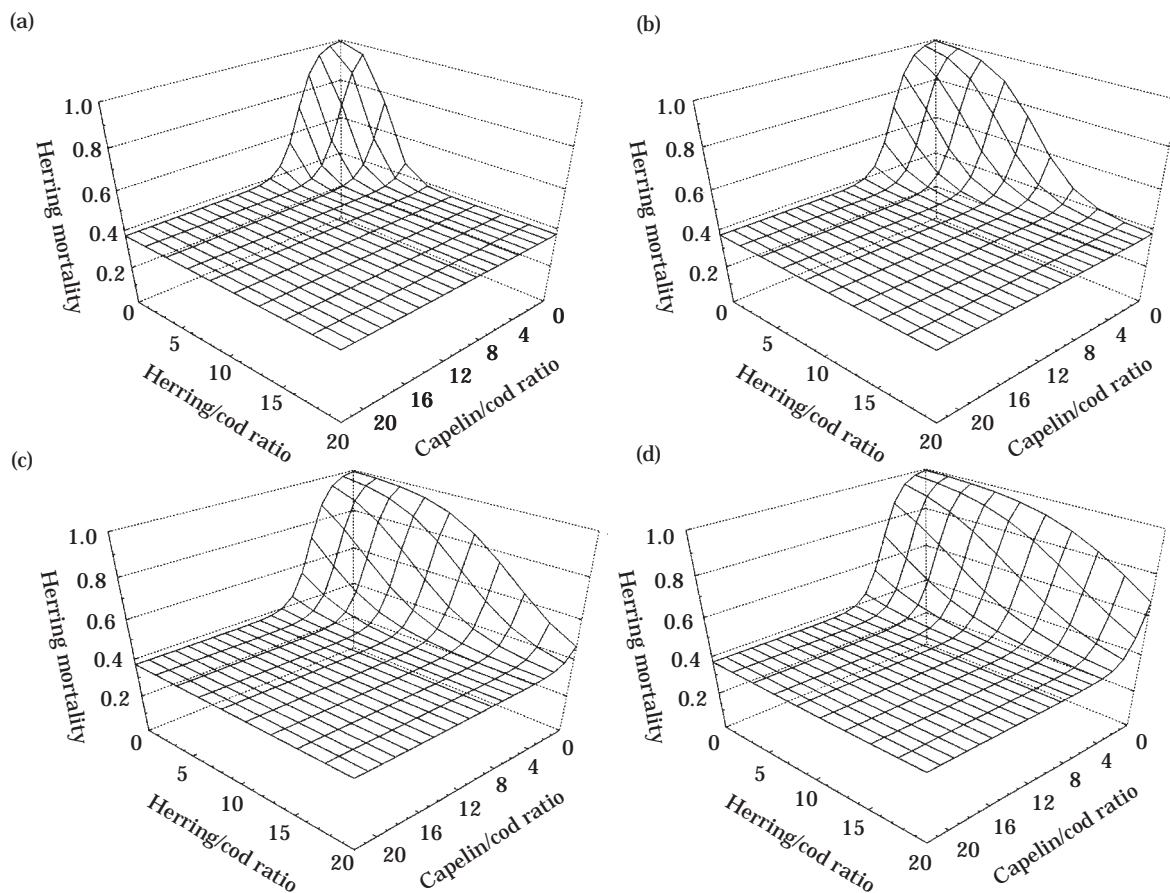
(a)

(b)

(c)

(d)

Figure 7. Hypothetical relationship between herring 0-group mortality and capelin/cod and herring/cod ratios: (a) coefficient of herring/cod ratio=coefficient for capelin/cod ratio; (b) coefficient of herring/cod ratio=1/2 of coefficient for capelin/cod ratio; (c) coefficient of herring/cod ratio=1/3 of coefficient for capelin/cod ratio; (d) coefficient of herring/cod ratio=1/4 of coefficient for capelin/cod ratio.

overlap between the prey and predator stocks, yet the results are in good agreement with the patterns expected from existing biological knowledge and ecological theory. This can be interpreted as indicating that the relative overlap between the three stocks considered here for the autumn remains approximately the same from one year to the next. The most likely explanation for this is that the three stocks will move more or less synchronously. No study has yet been conducted on quantifying the overlap of these three stocks during the part of the year of interest (O. Nakken, IMR, pers. comm.). Further work will be required before the actual influence of the variation in overlap can be assessed.

Other predators will also be important elements in determining the mortality of 0-group herring. Even if cod is considered the most important predator in the Barents Sea system, it is not the only one, and other stocks have been shown to prey upon young herring. The most important of these are probably marine mammals, especially minke whales and harp seals (Hamre,

1994). The results from recent research (Nilssen *et al.*, 1992, 1994; Haug *et al.*, 1993, 1994) have shown that both whales and seals can consume large amounts of herring and capelin, and therefore have the potential to influence herring mortality. To estimate this effect, however, is difficult.

It must be stressed that this study was based on data from a restricted time-period when the whole Barents Sea system was recovering from an extremely unbalanced situation due to the severe depletion of both the herring and the cod stocks (Nilsson and Hopkins, 1992; Hamre, 1994). It is therefore possible that other factors, not evident in the data set analysed, may become important in the future and reduce the predictive power of the aspects studied here.

Both the herring and cod stocks are now increasing (Hamre, 1994), and in recent years recruitment of 0-group herring has been at a much higher level than previously (Fig. 8). If the 0-group herring becomes abundant enough, it is therefore possible that a small
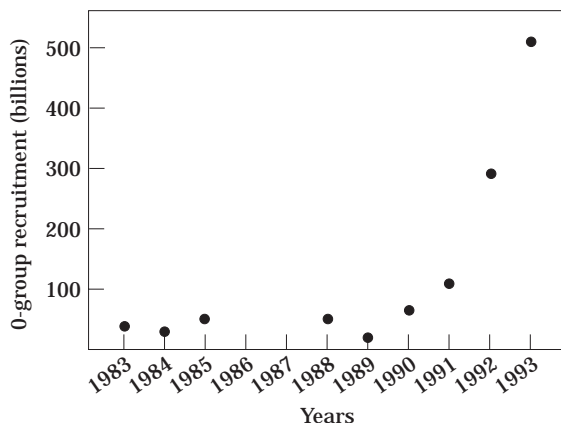
Figure 8. Estimated recruitment of herring to the start of the 0-group stage in the Barents Sea. Computed under the ''two-level survival model''.

part of the herring cohorts entering the Barents Sea in years of low relative capelin abundance will survive the predation by cod. The present situation of ''all or none'' survival would then shift to a larger variability of survival possibilities, due to predator swamping in years of very large 0-group herring abundance.

Another expected change may arise from the herring/capelin interaction described by Hamre (1994). Hamre has suggested that capelin recruitment is severely reduced in years when large or even only moderate amounts of juvenile herring are present in the Barents Sea, most probably due to predation from young herring on capelin larvae, and this hypothesis has been supported by the work of Huse and Toresen (1995). As the herring stock increases, the frequency of good capelin year-classes is therefore expected to decrease, and consequently the cod will turn to herring more. With a large cod stock and a depressed capelin stock, survival conditions for the herring will be very much reduced, and it is likely that the patterns in herring recruitment will resemble very much those observed before the collapse of the herring stock (Marti and Fedorov, 1963). The average interval between good year-classes will increase, and so will the importance of these for the state of the total stock.

Overall, this study confirms the importance of taking into account multispecies interactions when considering the dynamics of the herring stock, as it does for the capelin and the cod stocks (Mehl and Sunnanå, 1991; Tjelmeland and Bogstad, 1993; Ulltang, 1996).

Acknowledgements

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