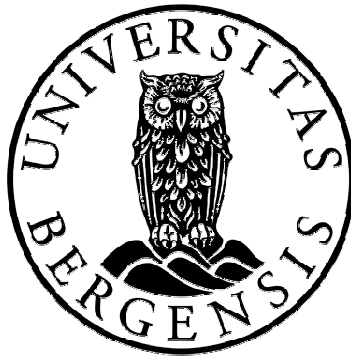# Influence of spawning stock size and environment on abundance and survival of juveniles in commercially important fish stocks in the Barents Sea

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Dissertation for the degree doctor scientarium (dr. scient.)

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Gjert E. Dingsør

Summary

Stock-recruitment relationships are fundamental in management of fish stocks and fish recruitment is highly variable. Hence, a mechanistic understanding of the factors causing the variability in recruitment is a necessity to be able to predict the development of a harvestable stock. To get continuity in the management it is also important to get an early indication of the size of future year-classes recruiting to the fisheries. Survey-based abundance indices are often used to assess the state of a fish stock and to predict the strength of future year-classes, it is therefore important that these estimates give a correct picture of the present state of the stock. However, both biotic and climatic factors are known to affect year-class strengths and these factors can exhibit nonlinearities and non-additive properties that are difficult to incorporate in traditional stock-recruitment models. My thesis consists of three papers focusing on I) estimation of abundance indices of 0-group fish in the Barents Sea, II) biotic and climatic effects on 0-group and age-1 abundances of capelin (*Mallotus villosus*), northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring spawning herring (*Clupea harengus*), and III) spatial variability in survival of 0-group northeast Arctic cod.

Survey data of 0-group fish in the Barents Sea are reviewed back to 1980, new abundance indices are estimated, and different methods for estimating abundance indices are evaluated. The new methods used to calculate the indices retain more of the dynamics in the annual recruitment than the previous methods do. The Pennington estimator method is concluded to be the preferable method for estimating 0-group indices for the Barents Sea. It is also attempted to correct for length-dependent selection properties of the trawl and it is shown that this bias affects both length and abundance estimates. However, it is concluded that more research is needed to quantify this bias under different environmental conditions before it is advisable to correct for it in the abundance indices.

Generalized additive modeling (GAM) and threshold GAM (TGAM) are applied in modeling the effect of biotic and climatic effects on the abundances at the 0-group and age-1 stages of capelin, northeast Arctic cod, northeast Arctic haddock, and Norwegian spring spawning herring in the Barents Sea. Spawning stock biomass, temperature, and density-dependent mechanisms are important factors affecting the year-class strengths of 0-group fish in the Barents Sea. The mean age of the cod spawning stock affects the abundance of 0-group cod, highlighting the importance of maintaining a diverse age-structure in the spawning stock. Cod, haddock, and herring have a similar response to temperature, which is possibly a proxy for available zooplankton. The results indicate that when strong year-classes are formed, the competition for food increases both within and between species. It is demonstrated that the intensity of density dependence can change over temporally distinct environmental phases. Density-independent factors may thus indirectly affect population dynamics through changes in density-dependent regulation. The complexity of interactions between biotic and climatic variables is difficult to incorporate in traditional stock-recruitment models. In such a context, the phase-dependent and nonparametric methodology of threshold generalized additive models has advanced our ability to address internal and external mechanisms in recruitment dynamics.

The abundances at age-1 are well correlated with 0-group abundances, indicating that year-class strengths at age-1 are determined prior to the 0-group survey in August-September. Predation by cod and temperature also affect age-1 abundances, and especially cod predation may affect the year-class strengths before they recruit to the fisheries, but in general strong year-classes will remain strong and poor will remain poor.

The climatic conditions and the density of predators show high spatial variability in the Barents Sea and it is thus plausible that the survival of 0-group fish also shows high spatial variability. With northeast Arctic cod as a case study, the spatial variability in survival is modeled using GAM and TGAM. The spatial pattern of 0-

group cod survival is primarily affected by top-down mechanisms and by predation-driven density dependence. Climate-related variables can strongly influence the spatial survival pattern of 0-group cod by affecting their distribution and the overlap with predators.

List of publications

This thesis is based on the following three papers and manuscripts. The papers are referred to in the text by their Roman numerals.

I. Dingsør, G. E. 2005. Estimating abundance indices from the international 0-group fish survey in the Barents Sea. Fisheries Research **72**:205-218

II. Dingsør, G. E., L. Ciannelli, K. S. Chan, G. Ottersen, and N. C. Stenseth. Density dependence and density independence during the early life stages of four large marine fish stocks. *Submitted manuscript.*

III. Ciannelli, L., G. E. Dingsør, B. Bogstad, G. Ottersen, K. S. Chan, H. Gjøsæter, and N. C. Stenseth. Spatial anatomy of species survival rates: effects of predation and climate-driven environmental variability. *Submitted manuscript.*

Contents

Synthesis

Influence of spawning stock size and environment on abundance and survival of juveniles in commercially important fish stocks in the Barents Sea

1. Background and objectives

The production of zooplankton at high latitudes is restricted to a relatively short period each year. This production is preyed upon by larvae and early juveniles of a number of fish species together with older capelin (*Mallotus villosus*) and herring (*Clupea harengus*). Zooplankton is thus converted to food for larger fish and animals, which are resources for fishing and hunting. A key question in respect to management is then: How to manage the resources to ensure that most of the yearly production of zooplankton results in commercially exploitable resources? Intuitively the answer is to ensure that the spawning stocks are large, because this will make sure that enough larvae and early juveniles are participating in the transformation of plankton to food for larger fish and animals. Hence, a mechanistic understanding of the spawning stock-recruitment processes is important within the study of population dynamics and management of fish stocks.

Most of the commercially important fish stocks in the Barents Sea and adjacent waters are spring spawners. The spawning grounds are mainly located along the Norwegian coast, close to shore or at banks, and along the continental slopes, but with rather wide distributions and differences between and within species. Eggs and larvae drift northwards in the upper layers by the coastal current and the north Atlantic current in the period April-July and end up in the Barents Sea and west of Svalbard. The abundance of 0-group (juveniles of the year) in the Barents Sea show large inter-annual variation and a stock's 0-group abundance appear to be exposed to periods of good years alternating with poor years. For northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring spawning herring these periods correspond to high and low temperature periods (Ottersen and Loeng 2000, Toresen and Østvedt 2000). It has also been shown that strong year-classes of cod and herring coincide with strong inflow of Atlantic water (Ottersen and Sundby 1995, Sundby 2000, Toresen and Østvedt 2000, Dippner and Ottersen 2001), and it is plausible that this strong inflow of Atlantic

water causes strong influx and high abundance of copepods in the drift routes of larvae and early juveniles, thus causes the prey availability to be better than in years with low or no inflow (Sundby 2000). The abundance of 0-group fish in the Barents Sea has been surveyed annually in August-September since 1965 (Anon. 2004). This time-series has been used in several recruitment studies for cod (Ottersen and Sundby 1995, Helle et al. 2000, Dippner and Ottersen 2001), while for the other species the time-series are primarily used to get an early insight to whether the year-class is poor, medium or strong.

Earlier the Area Index (AI) method (Haug and Nakken 1977) and the Logarithmic Index (LI) method (Randa 1984) were used to estimate abundance indices from the 0-group survey. The AI and LI methods are old and neither of them reflects the dynamics in the 0-group abundances to an adequate extent. It has also been shown that the sampling trawl used since the early 1980s is highly selective for 0-group cod and haddock (Godø et al. 1993, Hylen et al. 1995). Its capture efficiency of small individuals is much less than for bigger 0-group and this may lead to an annually variable bias since growth is positively correlated with temperature. Consequently, concern has been raised about the methods used to estimate 0-group indices as well as about the catching efficiency of the trawl for the smaller-sized fish. Improved methods for estimating abundance indices are available and computer resources are no longer a limiting factor when dealing with large datasets. Unfortunately, the 0-group survey data are not available in a computerized format prior to 1980.

During the period that 0-group fish have been surveyed in the Barents Sea, large variations have taken place in the environment, spawning stock biomasses, and age compositions of spawning stocks for all important species (Ottersen and Sundby 1995, Gjøsæter and Bogstad 1998, Dippner and Ottersen 2001, Fiksen and Slotte 2002). There exists several time-series of environmental variables as for example temperature, salinity, water flux, wind, and surface pressure, where some has been used regularly in single species analysis, for example the Kola temperature series (Dippner and Ottersen 2001). The possibility of identifying and quantifying the

importance of a variable environment for the abundance of 0-group fish is therefore good. For most species there also exists time series of the spawning stock biomasses and their age compositions, which makes it possible to analyze their importance to the abundance of 0-group fish.

The spawning stock-recruitment relationship is a fundamental concept in management of marine fish stocks. Most of these relationships used in management are based on the spawning stock biomass and the number of recruits to the fisheries. However, several studies have called attention to the danger of treating spawning stock biomass as an error-free independent variable in stock-recruitment analysis (Marshall et al. 1998, Marteinsdottir and Thorarinsson 1998). Condition, length, and age composition of spawning stocks are some of the factors affecting the realized fecundity. In addition, the numbers of recruits in most stock-recruitment relationships are estimated by cohort analysis, which is dependent on the official catch statistics. Errors in reported catches, caused by illegal fishing or discarding of small fish, may lead to a significant bias in the cohort estimates (Dingsør 2001, table 3.31 in ICES 2005). Consequently, survey based assessment of recruitment may be more reliable (Korsbrekke et al. 2001). For some stocks, the relationship between the spawning stock and the abundance at early life-stages, for example larvae, 0-group, and age-1, has also been analyzed. Especially for northeast Arctic cod there exist several such studies (Ottersen and Sundby 1995, Helle et al. 2000, Dippner and Ottersen 2001). However, an analysis where one investigates the co-variation in 0-group abundances between species has so far not been done.

The study of population dynamics in fisheries science has primarily evolved around temporal dynamics. For example, annual trends of a cohort survival are correlated with average values of biotic (predators, primary production, zooplankton density), or abiotic (temperature, wind speed, current field) factors. However, the variability in space of these factors is also likely to greatly affect the overall cohort survival. Spatial variability in individual survival is mediated by the location where the individual resides, and by the biological and physical properties typical of that area. It

follows that over the entire range of distribution of a single population, different individuals may experience different levels of environmental forcing and survival, which may not be well represented by average conditions throughout the entire spatial domain occupied by the population. The interplay between spatial and temporal dynamics has often been neglected in the fisheries literature and management. However, the conceivable spatial variability in fish survival speaks to the need to understand its causes and effects.

The objectives of this work have been to:

1. Establish improved time series for 0-group fish abundance in the Barents Sea that can be used in management of the stocks.

2. Evaluate the importance of spawning stock biomass, environmental forcing and interactions between species on the abundance of 0-group and age-1 of capelin, cod, haddock, and herring in the Barents Sea.

3. Estimate the spatio-temporal variability in the survival of northeast Arctic cod through their first winter of life (from 0-group to age-1).

2.   Methods for estimating abundance indices

Assessment of fish stocks is based on knowledge or assumptions about natural mortality, fishing mortality, growth, and recruitment parameters. All of these parameters are taken into account when trying to predict what will happen in the coming years. The purpose of fish stock assessment is to analyze a stock's development with different fishing pressure to maximize yield and ensure a sustainable fishery. Predictions of future recruitment are very important in forward projections of the stock and these predictions are often based on abundance estimates from surveys. Fish recruitment often shows high variability and uncertainty. As an example, it is worth mentioning that at the time when Randa published the Logarithmic Index (Randa 1984), he also performed a correlation analysis between the 0-group indices and VPA estimates at age-3 for cod and haddock. For the 1970-1976 year-classes the correlation was 0.92 for cod and 0.89 for haddock. Regression lines based on these correlations were used to predict year-class strength at age-3 and a too high confidence in these predictions contributed to the reduction of the cod stock in the late 1980s (Nakken 1994, Odd Nakken, IMR, pers. comm.). The 1983-1985 year-classes were strong at the 0-group stage, but the two last year-classes failed to recruit to the fisheries because of increased cannibalism which again was caused by the depleted capelin stock (Mehl 1991). The optimistic prognosis based on the 0-group indices lead to too high quotas and the combination of increased natural and fishing mortalities caused the reduction in the cod stock. Thus it is important to have reliable information of year-class strength as soon as possible. However, in long-term projections, one also needs to have knowledge about how biological and environmental variables affect year-class strength. With the exception of capelin, the 0-group survey indices in recent years have received little weight in assessment of fish stocks in the Barents Sea because of low correlation with numbers of fish recruiting to the harvestable stocks (Ulltang 1996, ICES 2005) and the experience from the 1980s. But why is this correlation so low? There are four possible explanations for this:

1. The methods used to calculate the abundance indices may be unreliable.

2. Survey estimates may be unreliable because of variable bias caused by poor catching efficiency of smaller-sized fish (Godø et al. 1993, Hylen et al. 1995) and near bottom distribution (Sundby et al. 1989).

3. Annually variable survival rates driven by density-dependent and density-independent variables may distort the relationship.

4. Recruitment estimates based on commercial catch statistics may be less reliable than survey based assessment of recruitment (Korsbrekke et al. 2001).

There exist several methods for estimating abundance indices and all of them have their strengths and weaknesses, and the best method may depend on the survey design, sample gear, and the species investigated. In Paper I two methods for estimating abundance indices were assessed. Method I was based on the stratified sample mean method where mean densities in each strata were weighted by strata area. Method II was the Pennington estimator, which is an estimator of the mean based on the lognormal distribution. The results from these two methods were similar, but method II was concluded to be preferable because the estimates were slightly more precise (Table 1) and because the occasional large catches and all the zero values do not affect the estimates of method II as much as they do in the case of method I (Pennington 1983, McConnaughey and Conquest 1993, Pennington 1996). The coefficient of variance (CV) can be used to assess the precision of an estimate and the CV for method II is slightly lower than the CV for method I in regards to cod, haddock, and herring, but the decrease in CV is non-significant. However, capelin show an increase in CV with method II and this may be caused by an underestimate of the variance by method I when there is an abundance of zero values (Pennington 1983).

16

Table 1 Mean and standard deviation (St.d.) of the Coefficient of Variance (CV) of 0-group indices estimated by different methods for the period 1980-2002, without correction for length-dependent selection (nlc) and with correction (lc). Methods I and II are Stratified sample mean and Pennington estimator from Paper I, respectively, and method III is Stratified sample mean from Anon (2005b).

Method	Cod Mean	Cod St.d.	Haddock Mean	Haddock St.d.	Capelin Mean	Capelin St.d.	Herring Mean	Herring St.d.
I nlc	0.25	0.09	0.20	0.05	0.34	0.14	0.40	0.13
II nlc	0.22	0.07	0.19	0.05	0.36	0.16	0.38	0.12
III nlc	0.24	0.08	0.19	0.06	0.34	0.15	0.40	0.14
I lc	0.23	0.08	0.19	0.05	-	-	-	-
II lc	0.21	0.06	0.19	0.05	-	-	-	-
III lc	0.23	0.08	0.19	0.06	0.34	0.15	0.40	0.12

In cooperation with Prozorkevich (PINRO, Murmansk) a new procedure for estimating abundance indices was developed (method III, Anon. 2005a, b). This procedure is based on the stratified sample mean method in Paper I, but the strata-system contains more and smaller strata and mean densities in each stratum are multiplied by stratum-area and summed, while in Paper I densities were weighted by stratum-area. When the covered survey-area is constant, it makes no difference whether the densities are weighted or multiplied by stratum-area because the ratio between the two indices is then constant. However, because the covered survey-area varies from year to year, this ratio is variable. The reason for not using the Pennington estimator is that it was agreed upon a strata-system with many small strata. The Pennington estimator is based on a lognormal distribution of sample values and the method requires a minimum of 20-30 stations in each stratum to be efficient (Pennington 1996). This requirement was not fulfilled with the new strata-system. However, little is gained by increasing the number of strata beyond six (Cochran 1977) and this is also confirmed in Table 1 and 2. This is supporting the conclusion of Paper I that the Pennington estimator is the most appropriate method for estimating abundance indices from the 0-group survey in the Barents Sea. Comparing methods I, II, and III with regards to precision, i.e. the coefficient of variance (Table 1), it is not possible to determine which method is the most appropriate. However, taking into account the effects that zero catches and occasional

large catches have on the precision and accuracy of the estimates based on methods I and III, it is concluded that method II is the best method.

By considering the correlation between abundance indices at two different life stages of a single species it is possible to assess the goodness of the different methods, although one has to be aware that variable mortality between the two life stages and the reliability of the second index will affect this correlation. The correlation between methods I, II, III, the Area Index (AI), the Logarithmic Index (LI) and indices at older ages (Table 2) show that there are no large differences between the new methods. It also shows that the new methods without correction for length-dependent selection reach a better correlation with age-1 indices than AI for all species but capelin, and that LI is the least accurate method. AI captures the trends fairly well, but as discussed in Paper I, much of the dynamic in the abundance from year to year is lost because of this method's smoothing properties.

Table 2 Correlations between 0-group indices estimated by different methods and abundance estimates at older ages for the period 1980-2002. Methods I and II are Stratified sample mean and Pennington estimator from Paper I, respectively, and method III is Stratified sample mean from Anon (2005b). Methods I, II, and III are without correction for length-dependent selection (nlc) and with correction (lc). AI is the Area index, LI is the Logarithmic index. BT stands for bottom trawl survey, VPA for virtual population analysis, and AC for acoustic survey.

	Cod		Haddock		Capelin	Herring
Method	Age-1 BT	Age-3 VPA	Age-1 BT	Age-3 VPA	Age-1 AC	Age-1 AC
I nlc	0.89	0.49	0.84	0.70	0.73	0.90
II nlc	0.89	0.50	0.84	0.70	0.74	0.90
III nlc	0.89	0.49	0.85	0.73	0.74	0.90
I lc	0.85	0.46	0.74	0.62	-	-
II lc	0.85	0.46	0.75	0.62	-	-
III lc	0.86	0.47	0.82	0.71	0.75	0.84
AI	0.86	0.45	0.79	0.65	0.82	0.73
LI	0.71	0.36	0.67	0.52	-	0.71

3. Bias in 0-group survey estimates

3.1 Length-dependent trawl selection

Abundance indices based on survey data will always be biased, because a sample gear does never give correct information over the entire range of densities and lengths of the surveyed species. Thus, survey based abundance estimates must be considered as relative indices and not absolute numbers. A constant bias will not affect the precision of the estimate and the accuracy may be assumed constant from year to year. However, if the bias is variable as for example the bias caused by length-dependent selection properties of the sampling gear when lengths of surveyed individuals varies from year to year, then this bias will cause the accuracy of the estimates to be variable and the time series to be less reliable.

The standard 0-group survey gear is highly selective for the smaller-sized fish (Godø et al. 1993, Hylen et al. 1995). Korsbrekke (1997) showed that this variable bias amounted to 3-9% and 10-50% overestimation of mean lengths of cod and haddock, respectively. This was also confirmed in Paper I. However, there are no previous investigations of the effect this bias has on the abundance indices. The correction functions established by Hylen et al (1995) were applied for cod and haddock in Paper I, while in later work correction functions estimated by Prozorkevich have been applied for herring and capelin as well (Anon. 2005a, b).

A correlation analysis between the 0-group indices, estimated by the different methods from Paper I and Anon (2005b), and abundance estimates at older ages for cod, haddock, capelin, and herring shows that for neither of the species does a correction for length-dependent selection improve the correlation (Table 2). These results indicate that the corrections introduce a reduction in precision or accuracy of abundance estimates. This may be caused by uncertainties in the correction functions themselves as well as uncertainties in the estimation of these. It is plausible that both

fish densities and temperature affects the selection properties of the trawl (Paper I). Consequently, the correction functions estimated for a single year may not be representative for all years. The corrections do not improve the precision of the abundance estimates, measured as coefficient of variance either (Table 1). Thus the main benefit of correcting for length-dependent selection seems to be a reduction of the bias in estimates of mean lengths. Similar conclusions were reached for corrections of estimates from the winter bottom trawl survey in the Barents Sea (Aglen and Nakken 1997).

In Paper I it was recommended that the length corrections were applied due to the variable bias in length estimates. Closer analysis of the abundance indices as discussed above revealed that there was no improvement in abundance estimates by using the length corrections and in Paper II we used the indices from method III (Anon. 2005a) without corrections. However, in the spatial analysis (Paper III) we found that the corrected densities gave the models a better fit. Thus, it is not possible to conclude either way, but it is recommended that the length correction functions are improved by further work before corrected indices are used in management.

3.2 Growth

Growth through the survey period may cause bias in estimates of mean lengths. With 0-group cod as an example, the mean length per station was modeled by a generalized additive model (GAM) with year as a factor and position and day of year as additive variables. The growth of 0-group cod was close to 0.9 cm in 24 days (Fig. 1), which gives a daily growth increment of 0.38 mm·d^{-1} and this is a conservative estimate compared to the growth rates (0.58-1.08 mm·d^{-1}) found during the two months preceding the 0-group survey (Loeng et al. 1995). Standardized cruise-lines starting in cold water and ending up in warm water may contribute to the increase in lengths. However, closer inspection of the cruise lines showed that they were fairly random

from year to year and that this effect is negligible. The growth causes the variance of estimated mean lengths to increase and this bias has increased the last years. The 0-group survey was originally conducted within three to four weeks in August-September. However, since this survey became part of an Ecosystem survey in 2003 the duration of the survey has increased and is now up to two months long, which is clearly not beneficial for mean length estimates and affects the reliability of the time series.
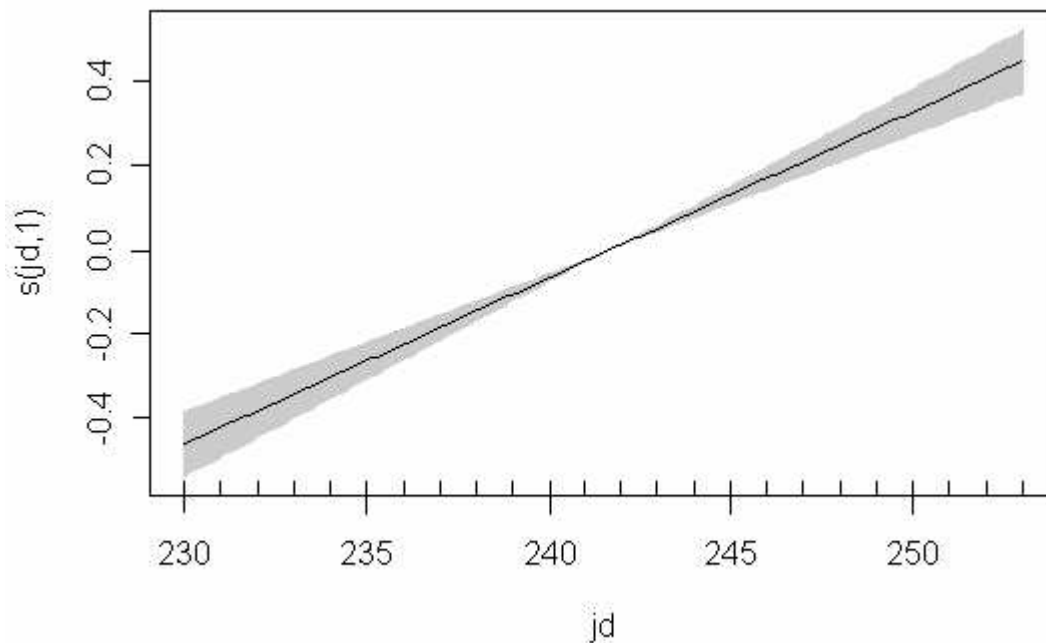
Figure 1 The effect of day of year (jd) on estimated length (cm) of 0-group cod, modeled by GAM. The shaded areas indicate approximate 95% confidence intervals of the modeled function. The model is corrected for year and position effects.

3.3 The settlement issue

One possible source of error that is often assumed to be negligible, but which there is not sufficient knowledge about, is the settlement of northeast Arctic cod and haddock. There is little information in the literature about when cod and haddock in the Barents Sea changes from a pelagic life-stage to a demersal life-stage. It is assumed that this transition occurs from late September through October for cod and

gradually throughout the autumn for haddock (Bergstad et al. 1987). Because of lack of knowledge about when settlement occurs, some authors have tried to use information gathered from other stocks. For example Mukhina et al. (2003) adapted information from cod stocks at Georges Bank, the Faroe Plateau, and the Baltic Sea and argued that cod in the Barents Sea settle when length is 4-8 cm, even though they noted that the mean lengths from the pelagic 0-group survey exceeded or overlapped with this range. Reviewing some of the literature on settlement of cod and haddock in other areas, it is apparent that it is not possible to generalize about when or at which length settlement occurs. For example at Georges Bank both cod and haddock have a gradual transition over 1-2 months when the fish are 4-10 cm long (Bowman 1981, Bolz and Lough 1988, Lough and Potter 1993), while haddock at the Scotian shelf (Koeller et al. 1986, Mahon and Neilson 1987) and cod at the coast of Nova Scotia (Tupper and Boutilier 1995) have a relatively abrupt transition when about 7-8 cm and <6 cm long, respectively. Similar differences are also described for the North Sea (see Lough and Potter 1993 for references).

Time of spawning and growth rate are found to affect the time of settling (Koeller et al. 1986, Hussy et al. 2003). In Norwegian coastal cod, the relationship between predator-induced mortality and growth seems to be one of the driving forces regulating the timing and size at settling (Salvanes et al. 1994). The presence of the large jellyfish *Cyanea* sp., which may serve as shelter, may delay the settlement of haddock (Koeller et al. 1986, Lough and Potter 1993). Mahon and Neilson (1987) suggested that in the transition period, haddock perform vertical migrations until they locate suitable bottom conditions and then become demersal. Thus, unsuitable bottom habitat may prolong the transition to demersal life. In northeast Arctic cod there also seems to be a difference between inshore and offshore segments of a year-class. Olsen and Soldal (1989) reported dense concentrations of small northeast Arctic cod located at or near the bottom in shallow water along the coast of Finnmark. In contrast, one year old cod in the Barents Sea have a pronounced diurnal vertical migration during winter, where temperature, bottom depth and predator density are factors affecting this migration (Hjellvik et al. 2004).

In summary, the timing and size at settlement of cod and haddock seems to be regulated by both biological and environmental factors where time of spawning, growth rate, food abundance, presence of predators and suitable habitats are important factors that may cause variation in settlement both spatially and temporally. The mean lengths of cod and haddock estimated in Paper I suggest that the majority settle later in the autumn and at longer lengths than more southern stocks, but one cannot disregard that some fish may have started to migrate towards the bottom at the time of survey and that this bias may vary annually. Evidence of this was seen in 2004 (Fig. 2) when a small section in the middle of the distribution area for cod was sampled two-three weeks later than the surrounding area and noticeable less cod was caught with the pelagic trawl in this section. To further illustrate this problem, 0-group cod densities were modeled by a threshold GAM where the Arctic Oscillation (AO) was used as a threshold variable (Fig. 3). When correcting for year and position effects there is a decreasing trend in cod densities with the day of year in a high AO regime (Fig. 3B), while in a low AO regime the effect is less (Fig. 3C), thus indicating that the migration towards the bottom is dependent on the surrounding environment and that it varies from year to year. However, this effect may also be caused by variation in mortality. Nevertheless, it illustrates the importance of synoptic survey coverage and that the start and magnitude of migration towards the bottom of cod and haddock need further investigation.
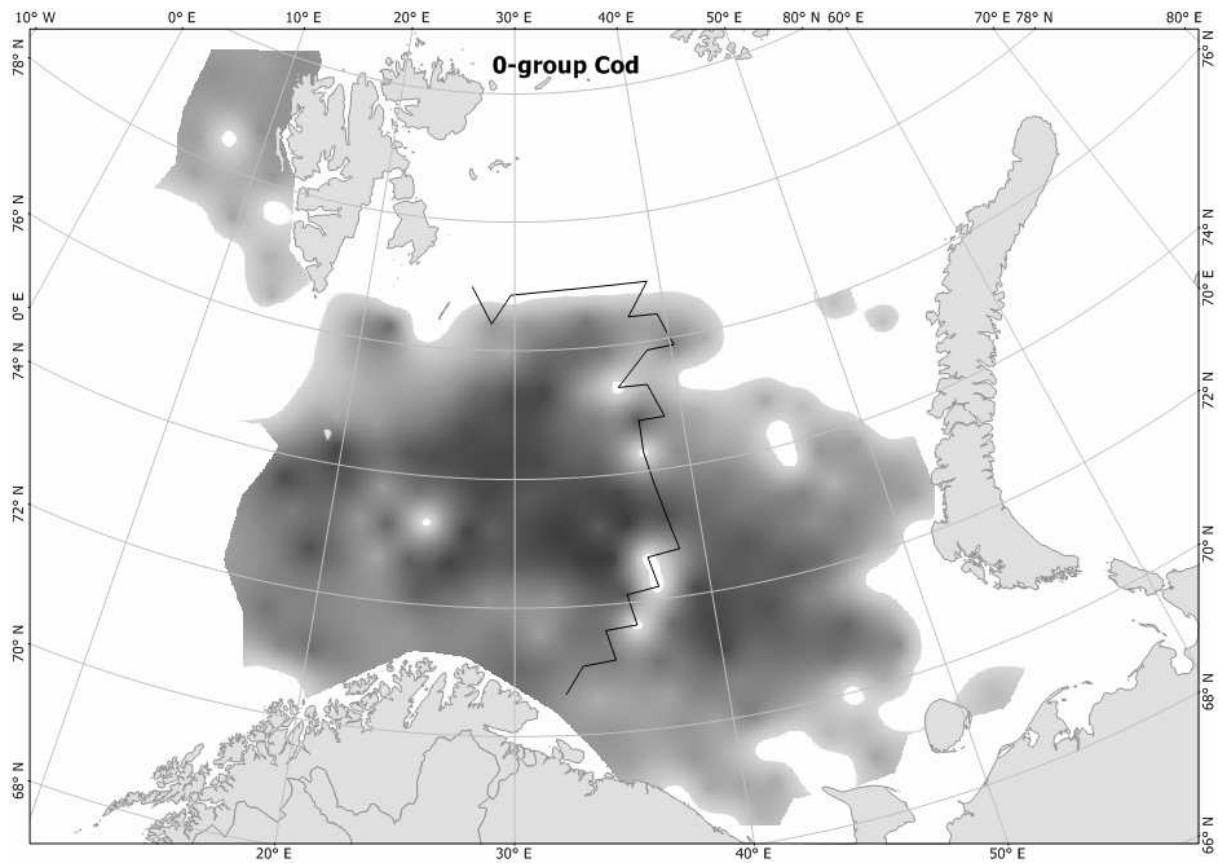
Figure 2 Distribution of 0-group cod in August-September 2004, dark areas correspond to high densities. The black line is the survey track of "Johan Hjort" September 13th – September 20th.
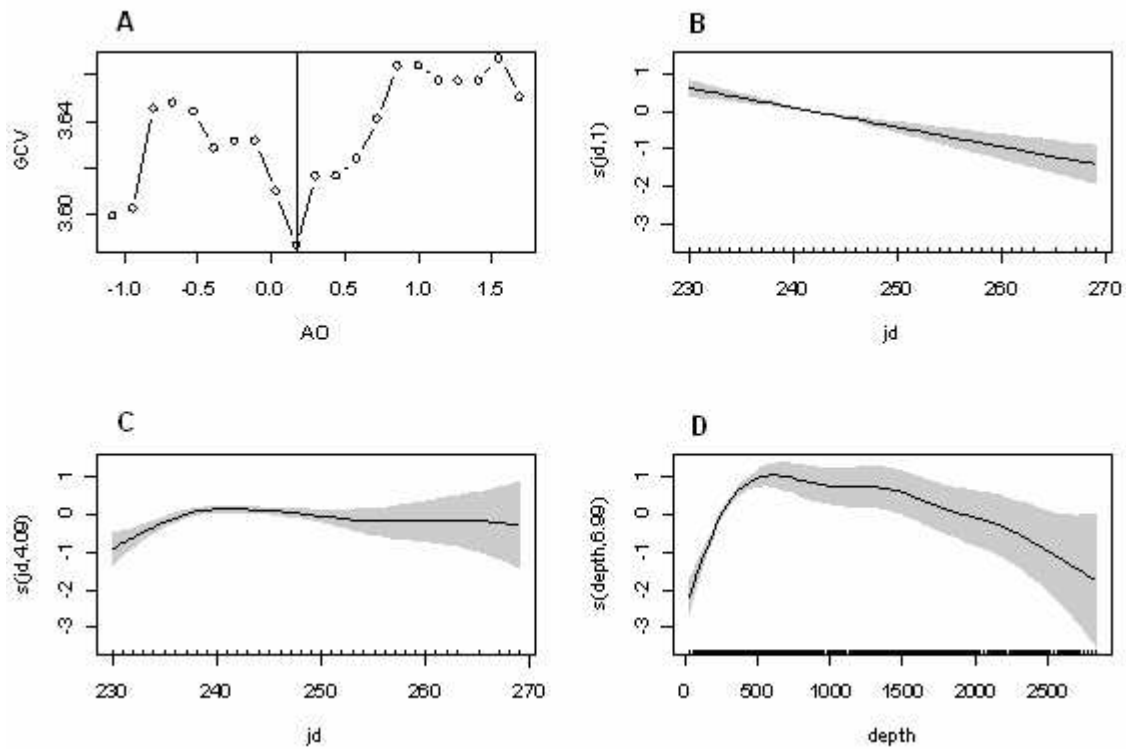
Figure 3 Modeled effect of day of year (jd) and bottom depth on catch rates of 0-group cod in a threshold GAM model. A) Threshold level of Artic Oscillation (AO). B) Effect of day of year on catch rates in a high AO regime. C) Effect of day of year on catch rates in a low AO regime. D) Effect of bottom depth on catch rates. The shaded areas indicate approximate 95% confidence intervals of the modeled functions. The model is corrected for year and position effects. Selection of threshold level is further explained in Appendix B to paper III.

4. Effects of spawning stock biomass and environment on 0-group abundance

Since the pioneering work by Hjort (1914), numerous scientists have tried to explain the causes of variation in year-class strength. Although progress is made, there is still a problem with predicting future recruitment (Govoni 2005). To be able to predict recruitment it is essential to be able to identify and understand the causal effects of recruitment variability. Many factors influence the abundance of 0-group fish in the Barents Sea. These include spawning stock biomass, maternal effects, climatic effects, predation, and zooplankton abundance. However, these factors may have complex interactive effects that are not easily incorporated into traditional stock-recruitment models. An example of this is the temperature threshold effect that influences the effect of spawning stock biomass on the abundance of 0-group herring (Paper II).

There are several stock-recruitment models (Needle 2002), but a common weakness with most of these is that they use spawning stock biomass alone as a measurement of potential fecundity. Several studies have questioned the reliability of spawning stock biomass as a measurement of potential fecundity (Kjesbu et al. 1998, Marshall et al. 1998, Marteinsdottir and Thorarinsson 1998, Marshall et al. 1999, Scott et al. 1999). Spawning stock biomass is in many cases the only available estimate of potential fecundity. However, in most managed fish stocks the age structure of the spawning stock is also available and this can be a valuable addition in a stock-recruitment model (Marteinsdottir and Thorarinsson 1998, Paper II). Nevertheless, spawning stock biomass is an important factor influencing year-class strength (Myers 2001, Paper II). For capelin, cod, haddock, and herring in the Barents Sea there is a positive relationship between spawning stock biomass and 0-group abundance (Paper II), but it was also found that the slope of this relationship depends on the spawning stock biomass and temperature. When the slope of this relationship decreases it is an indication of density-dependent survival, i.e. survival decreases as the abundance increases.

Density-dependent survival is commonly seen in fish populations (Myers and Cadigan 1993a, b, Paper II) and it is believed that strong density-dependent survival is operating at the juvenile stage, while stochastic density-independent survival is operating at the egg and larval stages as well as at the juvenile stage (Cowan et al. 2000, Myers 2001). Survival at the larval-stage is related to food-limited growth and may contribute significantly to recruitment variability, but it is most likely that density-dependent survival via feedback derived from reductions in prey resources occurs during the late-larval or juvenile stages (Cowan et al. 2000). Intra-cohort cannibalism has been suggested to be the main mortality factor after metamorphosis in rearing experiments of cod (Folkvord 1991, Folkvord and Otterå 1993). Cannibalism is related to food-limitations and Folkvord (1991) reported higher cannibalism rates among 0.2 g cod juveniles, which had higher daily growth rates, than among 8 g juveniles. From the analysis in Paper II it is not possible to determine when density dependence occurs. However, we found that density dependence in cod and herring is stronger prior to the 0-group survey than between 0-group and age-1. This may indicate that there is density dependence during the late-larval or the early juvenile stage, but it may also be caused by density-dependent reproduction caused by reduced fecundity due to competition for food in the spawning population. The strength of density-dependent survival was found to depend on temperature and it is believed that temperature acts as a proxy for zooplankton abundance, indirectly influencing survival (Paper II). Growth of early juveniles of cod, haddock, and herring is positively related to temperature (Loeng et al. 1995, Paper I) and the increased growth is a result of increased consumption and may lead to increased competition for food and generate density-dependent survival.

Temperature strongly affects 0-group abundance of cod, haddock, and herring (Ottersen and Sundby 1995, Ottersen and Loeng 2000, Dippner and Ottersen 2001, Paper I, Paper II). Increased growth and survival are influenced directly by temperature through increasing development rates and indirectly through increased abundance of the main prey (Sundby 2000, Ottersen and Stenseth 2001). Increased temperature also leads to increased competition between 0-group cod, haddock, and

herring, because of stronger year-classes. Competition between species has a negative effect on the abundance at the 0-group stage (Paper II). Other climatic factors that are shown to have an effect on survival of eggs and larvae are wind and flux of Atlantic water into the Barents Sea. Wind influences survival through turbulence and prey encounter rate (Fiksen et al. 1998, MacKenzie 2000) and through drift and advection of eggs and larvae (Ottersen and Sundby 1995, Sætre et al. 2002b). Flux is important for the abundance of zooplankton in the Barents Sea (Sakshaug 1997, Sundby 2000, Dalpadado et al. 2003) and the transport of larvae (Helle and Pennington 1999). Thus wind or flux may improve the models in Paper II.

Zooplankton is an important part of the diet for capelin, herring, and during the first years for cod and haddock. Growth of one and two year old capelin is positively correlated with the abundance of smaller zooplankton, mainly copepods (Gjøsæter et al. 2002). There is also a correlation between the distribution of early juvenile cod and the distribution of zooplankton; high concentrations of cod have a distinct overlap with high concentrations of zooplankton (Helle 1994, Helle and Pennington 1999). Early juvenile cod have limited ability to move over large distances in search of prey. Thus, the overlap between cod and zooplankton may be caused by the current patterns or by better cod survival in areas with high zooplankton concentrations. Zooplankton abundance is therefore another variable that we wanted to include in our models, but we were not able to find an appropriate time-series. On the other hand, zooplankton abundance at a given time may not correspond very well to the available prey experienced by the larvae and juveniles. This is because the zooplankton may be grazed down when there are a lot of juveniles in the Barents Sea, i.e. even though the production of zooplankton is high the abundance is low due to the strong predation pressure. There has not been found any positive relationships between zooplankton abundance and fish abundance in the Barents Sea. In fact, zooplankton abundance has an inverse relationship with capelin biomass, indicating that grazing by capelin has a negative effect on zooplankton abundance (Gjøsæter et al. 2002).

Several studies have suggested that predation from juvenile herring has a negative effect on the year-class strength of capelin (Hamre 1994, Gjøsæter and Bogstad 1998, Hjermann et al. 2004). Consequently, we tried to include the abundance of juvenile herring in our capelin 0-group model (Paper II), but we did not find any significant effect of herring. This may be caused by the correlation between the Barents Sea abundance of juvenile herring and the abundance of immature cod (age 3-6) in the studied period, immature cod was included in the model because they prey on the spawning capelin. However, even though stomach investigations of herring have confirmed that predation takes place, the rates were too low to explain the poor recruitment in the observed years (Huse and Toresen 2000). We did not find any negative effects of predation on the 0-group abundances from immature cod either. Thus it seems like predation has little effect on the abundance of 0-group fish in the Barents Sea. However we can not rule out that predation from other fish species, as for example blue whiting (*Micromesistius poutassou*), or from birds and whales may have a negative effect. For example the Atlantic puffin (*Fratercula arctica*) is an important top predator of 0-group herring (Sætre et al. 2002a).

5. Survival of 0-group fish

The first winter is believed to be an important period in defining the year-class strength in fish stocks of the Barents Sea. Individuals are confronted with a suite of survival challenges, including pre-winter condition, growth, predator avoidance, competition for food, and for cod and haddock, migration towards bottom and finding a suitable habitat. Climate-related variables can affect survival both temporally and spatially through temperature-dependent growth, abundance of available prey, and spatial overlap between predator and prey.

The abundance at age-1 of capelin, cod, haddock, and herring is well correlated with the abundance at the 0-group stage (Table 2), indicating that year-class strength at age-1 is defined prior to the 0-group survey in August-September. Capelin has the lowest correlation between the two ages, but this is expected since capelin has the longest time-span between the two surveys (one year). Contrasting to the other species, we find no relationship between 0-group and age-1 abundances of capelin at low temperatures (Paper II). This may be caused by stronger competition for food due to stronger capelin year-classes and reduced prey production at low temperatures. Cod and herring display a strong relationship between the abundances at the two ages, while haddock show a strong relationship at low temperatures, but no relationship at high temperatures. The lack of relationship for haddock at high temperatures may be caused by increased competition for food by strong year-classes of cod and herring. 0-group abundance of cod has a negative effect on herring age-1 abundance, which indicates competition for food between the two species.

Cod is the most important predator in the Barents Sea and capelin, cod, haddock, and herring are all preyed upon by cod (Bogstad et al. 2000). Capelin and cod age-1 abundances are significantly affected by predation by cod, while no significant effect was found on haddock and herring age-1 abundances (Paper II). The reason why we were not able to show this effect, even though we know that cod eats haddock and herring, may be related to the numbers we used to represent cod abundance. We used

VPA numbers of 3-6 year old cod, because they are believed to represent the majority of the fish eating cod population in the Barents Sea during winter. At this time, the mature cod have migrated out of the Barents Sea to spawn along the Norwegian coast (Bergstad et al. 1987) and younger cod (age 1-2) feed mainly on crustaceans and less on fish (Dolgov 2002, Dalpadado and Bogstad 2004). Previous studies have shown that predation by juvenile cod (age 1-3) and the capelin/cod ratio may affect survival of juvenile herring (deBarros et al. 1998, Johansen 2003) and these variables may thus be more representative for predation effects. However, if the mortality rates caused by cod predation are fairly constant we would not be able to detect this effect by the methods used because it would only affect the slope in the 0-group – age-1 relationship.

Paper III shows that there is large inter-annual and spatial variability in the survival of 0-group cod. The spatial variability in survival is strongly affected by cannibalism which is linked to temperature and the abundance of 0-group cod. Higher cod cannibalism at high temperatures may be caused by a more north and eastward distribution of older cod during such conditions (Nakken and Raknes 1987, Ottersen et al. 1998), and hence a higher spatial overlap between young and old cod. It is also shown that three year old cod is distributed further east when their abundance is high (Ottersen et al. 1998). Thus, both temperature and abundance of older cod has an effect on the survival of 0-group cod (Papers II and III). High temperatures have a positive effect on the abundance of age-1 cod, which is probably a result of the positive effect temperature has on 0-group abundance and the autocorrelation within temperatures (Paper II). In contrast, the spatial analysis shows that increasing temperatures have a negative effect on the survival of 0-group cod to age-1 (Paper III). The negative effect is most probably caused by increased cannibalism at high temperatures due to a greater encounter rate, rather than reduced survival due to resource limitation.

Are the survival estimates influenced by drift between the 0-group stage and age-1? Figure 4 shows the distribution of early juvenile and 0-group cod in 1984 when the

inflow of Atlantic water into the Barents Sea was medium (Helle and Pennington 1999). There is a north and eastward shift in the distribution during the period July-August, which is mainly caused by drift. It is possible that similar drift will affect the distribution of age-1 cod and hence the results of Paper III, depending on when the cod starts migrating towards the bottom and on active movement. Michalsen et al (1996) reported that vertical migration of young cod during winter was related with relatively strong east-going currents, ascending when current were strong and descending when current speed was decreasing. It is thus plausible that the vertical migration and strong currents may cause substantial horizontal displacement of cod during the period between 0-group and age-1 surveys, and this may explain some of the north and eastward displacement of high cod densities found in Paper III. Haddock and herring in the Barents Sea have a similar distribution to cod at the 0-group stage, but have a more south-western distribution compared to cod at age-1. This indicates that active movement is important in regards to age-1 distribution. Modeling of juvenile cod mortality has also shown that active movement away from older cod and into colder water give higher survival rates due to less cannibalism (Kristiansen et al. 2001). Consequently, drift and active movement may have affected the results of Paper III, but the main conclusions are still valid.
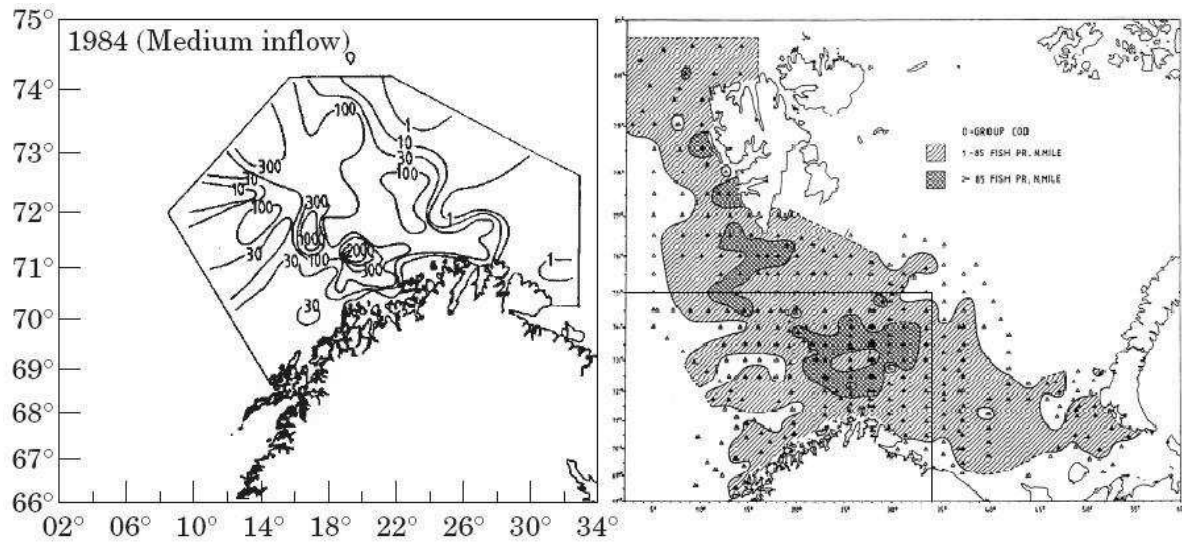
Figure 4 Difference in spatial distribution of early juvenile cod in June-July (left, from Helle and Pennington 1999) and 0-group cod in August-September 1984 (right, from Anon. 1984), mainly caused by drift. The frame in the right map shows the section of the left map.

6. Concluding remarks

The new 0-group indices are shown to retain more of the dynamics in the inter-annual abundance variability and are more appropriate to use in predictions of future recruitment to the fisheries, than the old indices. The 0-group survey has a good distribution-coverage of the important species of the Barents Sea, but it is recommended that a more synoptic coverage is strived for. Size-dependent selection properties of the sampling-trawl cause bias in length and abundance estimates. However, further selection experiments are needed to better quantify this bias under different environmental conditions before it is advisable to correct for it. The settlement-issue of cod and haddock is another area which needs further investigations.

Spawning stock biomass is an important factor affecting the year-class strengths of 0-group fish in the Barents Sea. For cod, the mean age of the spawning stock is also an important factor, highlighting the importance of maintaining a diverse age-structure in the spawning stock. Cod, haddock, and herring have a similar response to an increase in temperature, which influences growth and survival directly through increased development rates and indirectly through increased abundance of zooplankton. Indications of density dependence and interactions between species are shown, and may be caused by increased competition for food both within and between species when strong year-classes are formed. It is demonstrated that temperature can affect the intensity of density dependence in recruitment. Density-independent factors may thus indirectly affect population dynamics through changes in density-dependent regulation. The complexity of interactions between biotic and climatic variables is difficult to incorporate in traditional stock-recruitment models. In such a context, the phase-dependent and nonparametric methodology of threshold generalized additive models (TGAM) has advanced our ability to address internal and external mechanisms in recruitment dynamics.

Year-class strengths at age-1 are mainly determined prior to the 0-group survey in August-September, as seen from the strong correlations between 0-group and age-1. However, temperature affects density-dependent survival of 0-group capelin and haddock, and predation by cod affects the age-1 abundances of capelin and cod. Temperature affects the strength of cod cannibalism and this is most probably caused by a higher spatial overlap between young and old cod when temperatures are high. The spatial pattern of 0-group cod survival is primarily affected by top-down mechanisms and by predation-driven density dependence. Climate-related variables can strongly influence the spatial survival pattern of 0-group cod by affecting their distribution and the overlap with predators.

The present thesis has illustrated the complexity of recruitment dynamics in four important fish species in the Barents Sea. A lot of effort has been put into the improvement of the 0-group time series and the new indices are proven useful in the study of stock-recruitment dynamics. The strength of new statistical tools and spatial analysis are demonstrated and further application of these methods may improve our understanding of the Barents Sea ecosystem.

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Paper I

Estimating abundance indices from the international 0-group fish survey in the Barents Sea

ELSEVIER

Estimating abundance indices from the international 0-group fish survey in the Barents Sea

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Abstract

Annual abundance and distribution of 0-group fish in the Barents Sea have been recorded since 1965. Concern has been raised about the methods presently used to establish the abundance indices and about the catching efficiency of the trawl for the smaller-sized fish. The data have been reviewed for the period 1980–2002 and new abundance indices and length distributions of northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*), and redfish (*Sebastes* spp.) were estimated. The abundance indices were estimated by two different statistical techniques, the method of stratified sample mean and a method based on the lognormal theory. The latter method was concluded to be the preferred one for this particular survey. The poor catching efficiency of smaller cod and haddock was corrected for and the results showed that length dependent selection contributes to a serious bias in the estimates when not corrected for, and it is likely that selection will bias the estimates for the other species as well. It is recommended that the technique based on the lognormal theory and with length corrections becomes the new standard method for estimating abundance indices from the 0-group survey in the Barents Sea.

1. Introduction

Annually since 1965, the Institute of Marine Research (IMR) in Bergen, Norway, the Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Murmansk, Russia, and the United Kingdom (participated up to 1976) have conducted a joint international 0-group fish survey in the Barents Sea

and adjacent waters (Anonymous, 2002). The purpose of the survey is to give an early indication of the future recruitment to the fishable stocks of the most important commercial fish stocks in the Barents Sea. At present, two different abundance indices are estimated from this survey.

The "area index" (Haug and Nakken, 1977) is estimated for seven species. This method calculates two areas from a distribution map, the area of low density (catch rates) and the area of high density. The limit between low and high densities was established for each

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species separately based on a comparison of catch rates and echo recordings (Haug and Nakken, 1977), e.g. for cod the limit is 85 fish/nm. The abundance index is then estimated as follows:

$$AI = area\,(low) + 10 \times area\,(high) \tag{1}$$

This method has clearly some faults, the indices are smoothed and much of the dynamic in the time series is lost because 1 fish/nm will have the same influence as e.g. 80 fish/nm. Another problem is that there is no knowledge of the precision of the indices.

The second method is a logarithmic index and was developed by Randa (1984). This method is based on the lognormal theory. The catch rates are log transformed, mean densities are calculated for the 18 strata of which the area is divided into, the zero catches are handled separately, and the densities, weighted by stratum area, are summed. This method gives the indices on a logarithmic scale with confidence intervals. There are two problems with this method. The first is that small catch rates will produce negative values when they are log transformed and this may cause bias (Pennington, 1991; Kappenman, 1999). The second is that the indices are logarithmic and may in some cases cause problems in further analysis and interpretation of re-transformed means may be difficult.

The aim of this work is to produce a new set of 0-group abundance indices and length distributions for the most important commercial species in the Barents Sea, which are northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*), and redfish (*Sebastes* spp.). A few objectives were desired: the indices should be on an arithmetic scale and there should be some measurements of the precision of the estimates.

There are several more or less successful methods of estimating abundance indices and it seems there is no easy answer as to which method is most appropriate. In this work, two different methods are applied. The method of stratified sample mean, which is used on the bottom trawl survey for older fish in the Barents Sea, and an estimate of the mean based on lognormal theory, which in this paper will be called the Pennington estimator. The latter is an extension of the lognormal based estimator given in Pennington (1983, 1996). Both methods are described in Folmer and Pennington

(2000). Godø et al. (1993) and Hylen et al. (1995) showed that the trawl used in the 0-group survey has poor selection properties for the smallest fish and a correction factor is introduced for cod and haddock. Because of poor availability of computerized raw data prior to 1980, new indices and length frequencies are produced for the period 1980–2002.

2. Materials and methods

The data used in this work were extracted from the survey database at the Institute of Marine Research. The data were processed and analyzed using SAS software.

The 0-group survey in the Barents Sea has been carried out in late August–early September each year, using four to six vessels. Since 1980, Norway, and 1981, Russia, the trawling procedure has been standardized. The standard procedure consists of tows at three depths each of 0.5 nm, with the headline at 0, 20, and 40 m. Additional tows are made at 60 and 80 m if the 0-group layer is recorded below these depths with the echo-sounder. Most trawl stations are spaced apart by 30–35 nm sailed distance, but the distance between cruise tracks varies, and the distance between stations is in some cases less than 30 nm. The trawl used is a small-meshed mid-water trawl with 20 m vertical opening and 15 m wing spread (Godø et al., 1993). This sampling trawl has been used regularly since 1979 by Norwegian vessels and 1981 by Russian vessels. All Russian vessels in 1980 and one Russian vessel in 1982–1984 used a smaller sized (6 m × 10 m) trawl. Assuming that the catches are proportional to the area of the trawl mouth, the catches of the smaller sized trawl were multiplied by a factor of 3.33 to even out the difference in vertical opening. In 1994, one Russian vessel used a non standard trawl with 30 m vertical opening and unknown wing spread, two steps were trawled to cover the usual three steps.

Due to the trawling procedure, the effective trawling distance is equal to the total distance towed divided by the number of depth steps (Stensholt and Nakken, 2001). Because of many errors in the datasets, the total distances were recalculated. The duration of a trawl haul was found by the start and stop time, duration was then multiplied by the speed and the total distance was found. If the start time, stop time, or speed was miss-

ing, then the total distance from the data was used. Even though there is developed a coding system for the number of depth steps, these codes were often lacking or in some cases erroneous. Thus, the number of depth steps were found by the duration and the following criteria: 1 step when duration <16 min, 2 steps when duration is 16–25 min, 3 steps when duration is 26–35 min, 4 steps when duration is 36–45 min and 5 steps when duration is 46–55 min. If duration could not be calculated, the number of depth steps was found by total distance divided by 0.5 and rounded to the nearest integer. The effective distance, d_s, at station s was then found by

$$d_s = \frac{\text{total distance}}{\text{depth steps}} \tag{2}$$

The common practice in the old indices has been to use the effective distances of 1 nm for 2 steps and 1.5 nm for 3 or more steps (Havforskningsinstituttet, 1994). The reason for making the recalculations above even when values were not missing, is that the fewer

links of human touch between input and output, the smaller is the chance of human error in terms of calculation and punching errors.

The area covered by the survey was stratified into four strata (Fig. 1). Earlier in the logarithmic index they have used 18 strata, which is not very practical and usually little is gained in precision having more than six strata (Cochran, 1977). Fewer and larger strata results in larger sample sizes within a stratum, which results in more stable analyses and more varied analytical techniques can be used (Smith, 1988; Pennington, 1996). The new strata system has four strata and extends over a larger area than the previous. The strata are based on the distribution of trawl stations and on the species distribution maps from the survey reports. Strata I and II do normally have higher fish densities than III and IV, but this depends on the species.

To find the coverage of a stratum, the station positions were loaded into the GIS software; Manifold system 5.50. The boundary stations were traced and
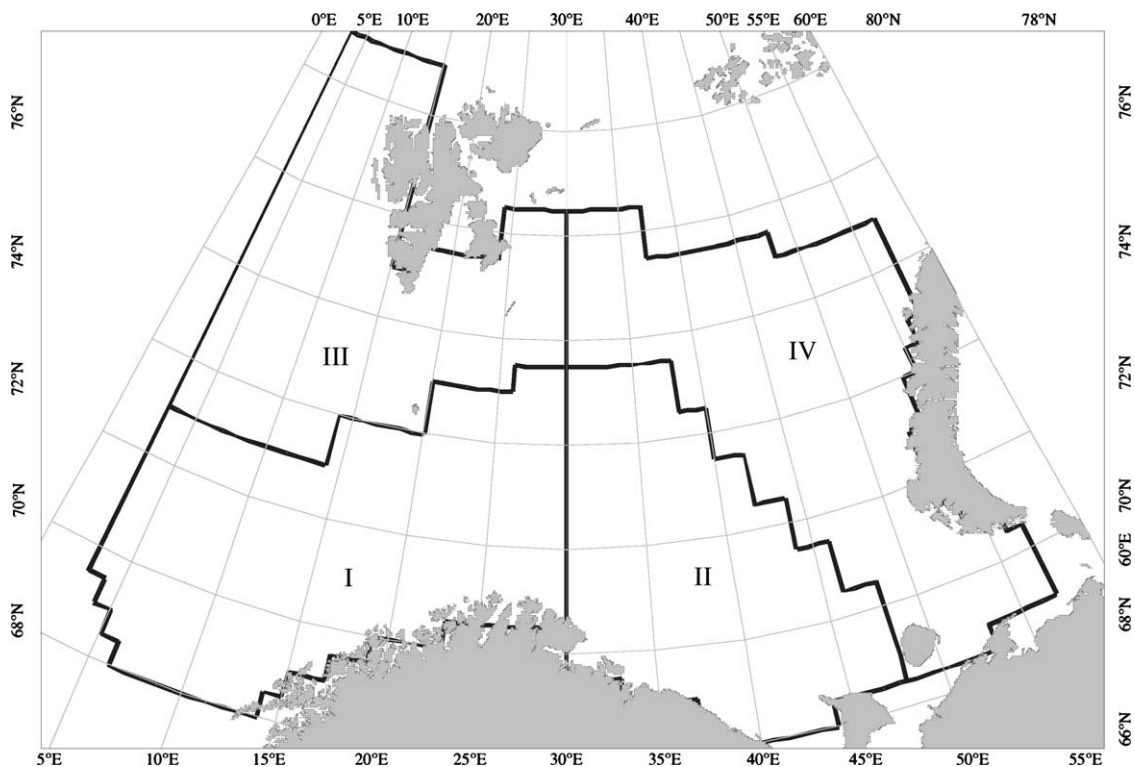

Fig. 1. The Barents Sea divided into four strata. The areas of strata I–IV are 143600, 104314, 111626, and 127747 nm^2, respectively.

Table 1
Coverage of strata and total area in percent

Year	Stratum I	Stratum II	Stratum III	Stratum IV	Total	
1980	88	76	63	15	61	
1981	56	78	67	25	55	
1982[a]	58	57	61	5	45	
1983	47	80	68	23	53	
1984[a]	50	15	54	1	31	
1985	63	81	69	28	59	
1986	48	81	57	28	52	
1987	52	83	52	23	51	
1988	63	78	56	18	53	
1989	56	86	60	75	68	
1990	55	91	57	46	61	
1991	52	91	63	63	66	
1992	46	75	65	35	54	
1993	43	84	54	37	53	
1994	35	82	42	31	46	
1995	45	76	41	12	42	
1996	45	91	45	47	56	
1997	41	86	34	32	47	
1998	37	88	41	62	55	
1999	38	85	36	51	51	
2000	50	85	49	51	58	
2001	49	87	57	70	64	
2002	48	85	48	49	56	
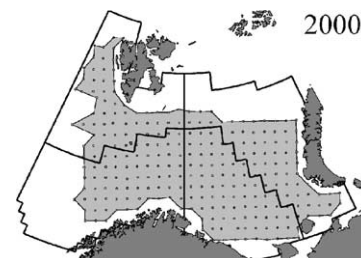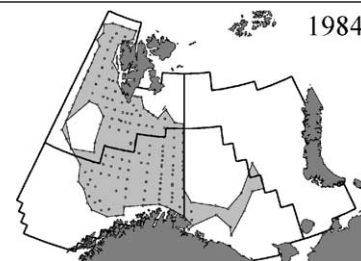
1984 and 2000 are examples of poor and good coverage (inserted figures).

[a] Russian data are missing.

the areas enclosed were calculated. The conic projection Albers equal-area, with center latitude at 74°N, center longitude at 30°E, and standard latitudes at 70° and 78°N, was used in this operation. The coverage varies to a large extent from year to year (Table 1). In 1982 and 1984, the low coverage is due to a lack of Russian data in the IMR database.

To minimize the chance of including older age groups in the analysis, maximum lengths were defined for each year and species. This was done by going through the survey reports and finding the maximum lengths from the length frequency tables. Most length data are also coded with age codes and all data that were coded older than 0-group were excluded from the analysis. Erroneous coding and coding that includes both 0-group and older fish will cause bias when the length distributions of 0- and 1-group overlap. Minimum length was set to one centimeter.

The data were also quality checked. Only ordinary fishing stations with pelagic trawl hauls of satisfac-

tory quality and gear in good condition were included. Longitude and latitude were checked by plots of trawl station positions with survey tracks, compared by eye with maps in the survey reports and corrected by original station forms if large discrepancies were detected.

Godø et al. (1993) showed that the sampling trawl is highly selective for 0-group cod and haddock. Its capture efficiency of fish smaller than 65 mm was much lower than their experimental trawl. Hylen et al. (1995) used data from a similar experiment to estimate the following correction functions, $w(l)$, for cod and haddock

$$w(l)_{cod} = 1 + \exp(4.158 - 0.422 \times l) \tag{3}$$

$$w(l)_{haddock} = 1 + \exp(8.031 - 0.838 \times l) \tag{4}$$

where l is the length in cm. These correction functions can be applied directly to the observed length frequencies at each station. But since the functions above give unreasonably high numbers as l decreases, it was decided to set $w(l)_{cod}$ constant to 10 for $l < 4.6$ cm and

$w(l)_{haddock}$ constant to 20 for $l < 6.1$ cm. The fact that there were very few fish below these lengths in the datasets used to estimate the correction functions, supports this decision. The correction function, $w(l)$, was set to one for species other than cod and haddock, and in the cases where the non standard Russian trawls were used.

2.1. Stratified sample mean estimator

The number of fish per nm^2, $\rho_{s,l}$, at length, l, at each station, s, were estimated by the following equation:

$$\rho_{s,l} = \frac{f_{s,l}w(l)}{a_s} \tag{5}$$

where $f_{s,l}$ is the calculated frequency of length l at station s, $w(l)$ is the length correction function defined above, and a_s is the swept area found by

$$a_s = \frac{d_s \mathrm{ws}}{1852} \tag{6}$$

where d_s is the effective trawl distance found by Eq. (2), and ws is the wingspread of the trawl.

The stratified estimator of mean density in the entire area is given by

$$\bar{y}_{st} = \sum_{i=1}^{L} W_i \bar{y}_i \tag{7}$$

where L is the number of strata, W_i the proportion of the survey area in the ith stratum, $y_{i,s}$ is the sum of the densities found at station s by Eq. (5), and $\bar{y}_i$ is the average density in stratum i. The estimated variance of the stratified mean $\bar{y}_{st}$ is

$$\mathrm{var}(\bar{y}_{st}) = \sum_{i=1}^{L} W_i^2 \frac{s_i^2}{n_i} \tag{8}$$

where

$$s_i^2 = \frac{\sum_{s=1}^{n_i}(y_{i,s} - \bar{y}_i)^2}{n_i - 1} \tag{9}$$

The standard error of $\bar{y}_{st}$ is given by

$$\mathrm{se}(\bar{y}_{st}) = \sqrt{\mathrm{var}(\bar{y}_{st})} \tag{10}$$

2.2. Pennington estimator

The patchy distribution of marine organisms causes the sampled densities to have a skewed distribution with many small values and a few very large values. Thus, the sample mean may be an imprecise estimator of the true mean (Pennington and Strømme, 1998). An estimator of the mean based on the lognormal distribution is shown to be more efficient (Pennington, 1983, 1996; Smith, 1988). The 0-group data do usually have a cluster of small values and because values close to zero may severely bias lognormal-based estimators (Myers and Pepin, 1990; Pennington, 1991; Kappenman, 1999) an extension of the estimator in Pennington (1983, 1996), developed by Folmer and Pennington (2000), was used.

The values larger than the cut-level k in each stratum are supposed to be distributed approximately lognormal. The alternative estimator, $\hat{\mu}_i$, of mean density within each stratum is then given by

$$\hat{\mu}_i = \frac{n_i - m_i}{n_i} \bar{y}_i' + \frac{m_i}{n_i} \exp(\bar{x}_i) G_{m_i}\left(\frac{s_{x,i}^2}{2}\right) \tag{11}$$

where m_i is the number of sample values greater than k in stratum i, $\bar{y}_i'$ is the mean of the values smaller or equal to k, $\bar{x}_i$ and $s_{x,i}^2$ are the mean and variance of the logged sample values greater then k, and $G_m(t)$ is an infinite series function of m and t (for example, $m = m_i$ and $t = \frac{1}{2}s_{x,i}^2$) defined by

$$G_m(t) = 1 + \frac{m-1}{m}t$$
$$+ \sum_{j=2}^{\infty} \frac{(m-1)^{2j-1}t^j}{m^j(m+1)(m+3)\cdots(m+2j-3)j!} \tag{12}$$

The variance of $\hat{\mu}_i$ is given by

$$\mathrm{var}(\hat{\mu}_i) = \mathrm{var}(c_i) + \left(\frac{n_i - m_i - 1}{n_i(n_i - 1)}\right) s_i'^2$$
$$+ \left(\frac{m_i(n_i - m_i)}{n_i^2(n_i - 1)}\right) \bar{y}_{i'}^2$$
$$- 2\left(\frac{n_i - m_i}{n_i(n_i - 1)}\right) \bar{y}_i' c_i \tag{13}$$

where $s_i'^2$ is the variance of the values less than or equal to k,

$$c_i = \frac{m_i}{n_i}\exp(\bar{x}_i)G_{m_i}\left(\frac{s_{x,i}^2}{2}\right) \tag{14}$$

and

$$\text{var}(c_i) = \frac{m_i}{n_i}\exp(2\bar{x}_i)\left\{\frac{m_i}{n_i}G_{m_i}^2\left(\frac{s_{x,i}^2}{2}\right)\right.$$
$$\left. - \frac{m_i-1}{n_i-1}G_{m_i}\left(\frac{m_i-2}{m_i-1}s_{x,i}^2\right)\right\} \tag{15}$$

There is no single objective criterion upon which to define a cut-level, k, bigger than zero. For the 0-group data a value of k for a stratum equal to 20% of the average density in that stratum provided a cut-level such that the values larger than k are distributed approximately lognormal. The coefficient of variance (CV) was also used to find the cut-level. The trick was to find a cut level that gave low CVs without violating the assumption of lognormal distributions. The stratified estimate of mean density, $\hat{\mu}_{st}$, in the entire area is calculated by replacing $\bar{y}_i$ with $\hat{\mu}_i$ for each stratum in Eq. (7). The standard error of $\hat{\mu}_{st}$ is obtained by substituting $\text{var}(\hat{\mu}_i)$ for s_i^2/n_i in Eq. (8), and then

$$\text{se}(\hat{\mu}_{st}) = \sqrt{\text{var}(\hat{\mu}_{st})} \tag{16}$$

2.3. Length distributions

Another objective of the 0-group survey is to estimate the length distributions of the juveniles of the year. One way to do this is to use a variation of the ratio estimator, $\hat{R}$, of the mean length given by Cochran (1977)

$$\hat{R} = \frac{\sum_{s=1}^{n} y_s \bar{x}_s}{\sum_{s=1}^{n} y_s} \tag{17}$$

where y_s is the sum of the densities estimated by Eq. (5) at station s, $\bar{x}_s$ is an estimate of the average length of fish at station s, and n is the number of stations where fish of the species in question were caught. An estimate of population variance, σ_x^2, of lengths can be found by modification of the grouped sample variance

(Bhattacharyya and Johnson, 1977)

$$\hat{\sigma}_x^2 = \frac{\sum_{s=1}^{n}\sum_l \rho_{s,l}(l - \hat{R})^2}{\sum_{s=1}^{n}\sum_l \rho_{s,l}} \tag{18}$$

where $\rho_{s,l}$ is the density of fish of length l at station s.

3. Results

3.1. Abundance indices

Abundance indices of 0-group cod, haddock, capelin, herring, and redfish were estimated by the method of stratified sample mean and the Pennington estimator (Table 2). With few exceptions, there were no large differences between the two methods. When large differences occurred between the indices, for example capelin and redfish in 1982, the sample mean, $\bar{y}_{st}$, was mostly larger than the Pennington estimator, $\hat{\mu}_{st}$. Generally, the Pennington estimator was more precise than the sample mean, i.e. $\text{se}(\hat{\mu}_{st})$ was smaller than $\text{se}(\bar{y}_{st})$.

The length correction had a large influence on the abundance indices of cod and haddock. For both species there was a negative correlation between the index without length correction and the ratio: index with length correction/index without length correction, and for haddock this was significant ($p < 0.05$). This resulted in that the ratio: best year/worst year, got smaller when length correction was applied.

Cod had all the above average year-classes in the 1990s and in year 2000, this applied to the results from both with and without length correction. Without length correction, haddock had most of the good year-classes in the 1990s and 2000s. When length correction was applied, there were three good year-classes in both the 1980s and 1990s, and in year 2000. With the exception of 1983, herring had all the above average year-classes after 1990. With the exception of 1997 and 1999, capelin had the above average year-classes in the 1980s. Redfish had all the above average year-classes prior to 1991.

3.2. Mean lengths

Mean lengths with corresponding population standard deviations are shown in Fig. 2. There were no significant differences in mean lengths of cod with and

Table 2
Abundance indices based on stratified sample mean estimator ($\bar{y}_{st}$) and Pennington estimator ($\hat{\mu}_{st}$) with corresponding standard errors

Year	Cod without length correction				Cod with length correction				Haddock without length correction				Haddock with length correction			
	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)
1980	0.27	0.05	0.26	0.04	1.60	0.31	1.55	0.27	0.32	0.06	0.31	0.06	3.50	0.68	3.46	0.70
1981	0.23	0.04	0.22	0.04	1.55	0.24	1.54	0.25	0.06	0.02	0.06	0.01	0.81	0.24	0.73	0.17
1982	2.90	0.47	2.81	0.42	17.17	2.67	16.81	2.44	3.05	0.45	3.11	0.51	29.40	4.30	29.64	4.81
1983	19.23	5.52	15.37	2.84	74.91	18.57	62.01	9.88	5.97	1.04	5.65	0.83	33.52	4.61	32.65	4.23
1984	44.27	19.70	30.28	8.21	168.14	65.80	120.23	28.74	8.79	1.66	7.99	1.22	51.84	9.11	49.18	8.09
1985	64.57	16.57	55.92	11.28	266.17	69.73	229.86	43.29	2.81	0.63	2.66	0.65	15.76	2.85	15.80	3.54
1986	7.73	1.33	7.34	1.40	45.65	8.02	42.62	7.85	2.42	0.47	2.25	0.43	19.61	3.94	18.32	3.65
1987	0.68	0.15	0.61	0.10	5.17	1.23	4.53	0.71	0.55	0.12	0.51	0.10	9.62	2.09	8.92	1.76
1988	2.29	0.51	1.97	0.38	13.01	2.94	11.51	2.34	1.67	0.52	1.42	0.33	16.40	5.49	13.89	3.36
1989	2.73	0.69	2.36	0.43	10.27	2.34	9.12	1.52	0.64	0.11	0.62	0.10	4.78	0.81	4.41	0.69
1990	29.31	7.01	26.32	5.46	96.21	21.21	85.62	17.90	4.92	0.68	4.67	0.67	16.49	2.33	15.70	2.29
1991	45.32	6.74	42.75	6.38	160.75	23.45	151.97	21.76	15.74	2.23	15.30	2.07	101.91	13.64	97.87	12.86
1992	220.32	50.53	214.94	50.16	753.36	171.87	742.82	178.30	7.87	1.19	7.27	1.09	26.97	5.08	22.80	3.50
1993	166.01	47.84	157.14	46.30	517.98	136.08	491.78	133.56	5.73	0.92	5.58	0.91	14.10	2.14	13.67	2.01
1994	215.92	62.16	186.01	49.55	583.63	160.56	501.99	124.71	15.05	4.16	13.24	3.30	39.21	8.19	37.98	8.13
1995	426.51	98.22	408.23	80.17	1120.69	272.20	1058.81	207.77	2.61	0.58	2.60	0.60	6.66	1.41	6.37	1.33
1996	317.18	55.00	319.34	56.44	1178.94	205.53	1181.18	204.14	5.07	0.79	5.02	0.85	11.22	1.52	11.53	1.80
1997	389.09	55.48	403.53	64.71	1706.05	236.72	1781.03	286.40	3.38	0.54	3.52	0.67	15.76	2.79	15.60	2.79
1998	32.53	6.17	32.60	6.64	103.24	17.88	105.13	21.01	26.06	4.65	25.84	4.76	65.99	9.96	65.80	10.53
1999	6.57	3.06	6.05	2.96	18.46	7.07	16.79	7.25	5.63	1.97	4.89	1.73	13.94	3.99	12.16	3.13
2000	113.84	29.89	105.07	27.80	467.19	123.23	426.62	106.23	13.04	2.84	12.80	2.96	92.94	21.25	90.04	22.08
2001	3.32	1.41	2.24	0.63	16.51	7.03	11.57	3.45	7.50	1.45	7.26	1.45	24.66	3.76	24.72	4.11
2002	83.93	18.42	76.99	14.76	139.72	26.15	130.09	24.53	7.51	1.21	7.42	1.26	22.08	5.10	22.95	6.91

Year	Caplin				Redfish				Herring			
	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)	$\bar{y}_{st}$	se($\bar{y}_{st}$)	$\hat{\mu}_{st}$	se($\hat{\mu}_{st}$)
1980	1173.64	213.44	1294.47	300.02	779.07	560.15	663.36	433.57	0.02	0.01	0.02	0.01
1981	519.05	126.43	500.98	118.07	697.80	543.96	634.92	448.02	0.01	0.01	0.01	0.01
1982	1177.59	458.83	893.82	281.95	850.53	439.39	583.06	151.83	0.35	0.16	0.21	0.07
1983	419.38	97.58	356.23	66.73	212.20	53.07	188.84	39.97	125.45	40.02	128.30	42.26
1984	417.05	99.89	411.94	104.18	295.54	115.57	258.01	95.01	33.63	12.42	35.83	15.55
1985	99.73	45.93	74.64	30.03	1190.45	404.48	1040.96	399.19	24.65	10.69	31.52	19.61
1986	52.16	25.42	57.07	34.21	375.53	187.63	270.46	93.27	0.03	0.01	0.02	0.01
1987	2.91	1.24	3.13	1.59	88.78	24.31	81.73	21.14	0.01	0.00	0.01	0.00
1988	130.27	50.54	97.82	30.68	300.58	56.87	281.68	55.96	38.35	12.35	54.12	24.81
1989	923.71	95.34	944.57	108.10	62.07	19.25	47.03	9.63	15.98	5.66	11.89	3.40
1990	137.66	24.26	145.39	28.02	365.48	81.02	368.74	88.20	20.69	11.08	19.22	9.28
1991	234.14	69.32	269.23	123.17	111.23	48.44	105.52	49.12	407.91	127.14	340.82	87.33
1992	0.35	0.20	0.40	0.28	45.99	37.74	21.16	10.40	172.29	35.67	176.53	41.97
1993	0.89	0.32	0.71	0.23	24.18	18.26	13.27	6.59	283.60	123.52	243.21	103.73
1994	43.22	21.66	37.38	20.11	188.50	112.51	143.68	72.44	95.04	55.62	93.94	59.93
1995	2.61	1.61	2.67	1.63	65.18	24.96	68.03	27.02	12.77	5.03	10.56	3.30
1996	214.50	53.69	206.94	64.29	0.12	0.04	0.11	0.03	253.18	67.00	250.32	67.26
1997	308.40	86.50	277.73	66.93	0.76	0.43	0.53	0.25	247.32	63.98	249.68	73.45
1998	163.82	31.04	156.45	32.90	3.56	1.77	3.25	1.77	402.72	90.55	378.54	80.26
1999	403.75	104.93	354.68	77.03	0.16	0.05	0.16	0.05	81.74	37.96	73.05	28.37
2000	155.13	79.65	145.68	79.35	33.18	22.06	24.74	16.28	229.12	113.33	208.16	95.64
2001	19.08	8.35	18.71	8.68	0.02	0.01	0.02	0.01	3.24	1.45	2.48	0.87
9009	85.15	19.95	81.05	19.61	0.55	0.25	0.54	0.24	99.87	23.43	107.97	29.48

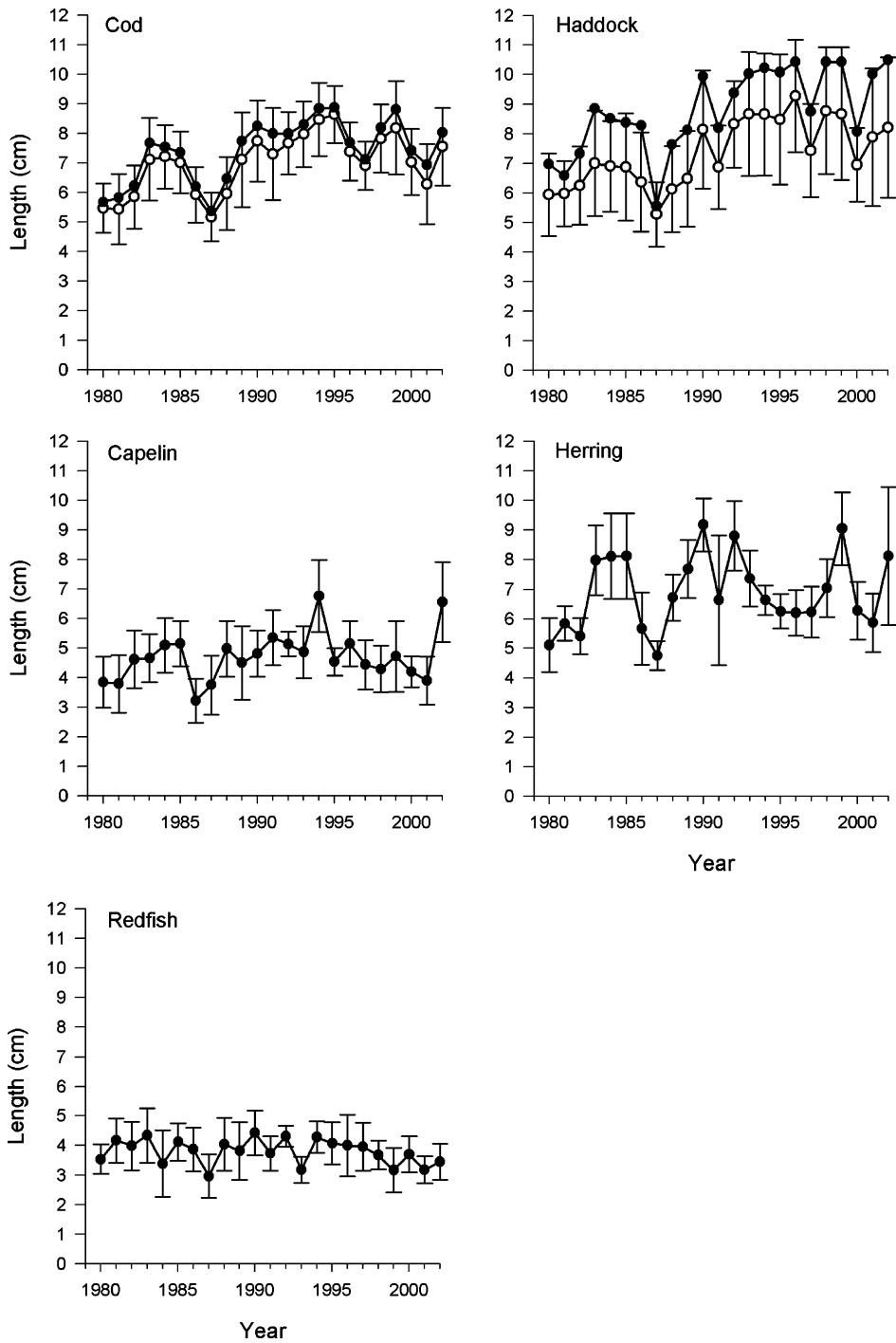Estimates are given in thousands per square nautical mile.

Fig. 2. Estimated mean lengths with population standard deviation. Open circles (cod and haddock) are estimates with length correction and the filled circles are without length correction.
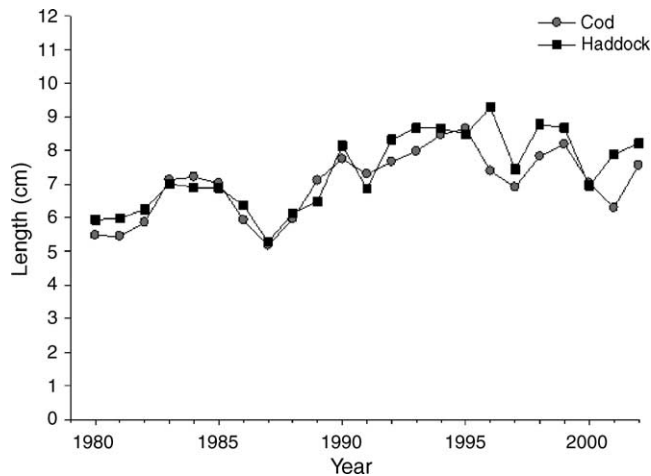
Fig. 3. Estimated mean lengths of cod and haddock after length correction.

without length correction, but the average of the mean lengths was lowered from 7.42 cm, without length correction, to 7.01 cm, with length correction.

Haddock had a significant decrease ($p < 0.01$) in mean lengths after length correction, and the average of mean lengths decreased from 8.81 to 7.37 cm. Mean lengths of cod and haddock became more similar when length correction was applied (Fig. 3), although haddock had larger standard deviations (Fig. 2). Both species had similar trends and were significantly ($p < 0.01$) larger in the 1990s than in the 1980s.

Mean lengths of capelin were smaller ($p < 0.05$) in the 1980s than in the 1990s, but this might be misleading because of the high mean length in 1994, which was caused by an overlap in lengths of 0- and 1-group capelin. This can also be a problem in 2002, but for this year there were no age-determined lengths to verify this. The remaining years, most of the means were close to the average mean length of 4.71 cm.

Herring had no difference in mean lengths between the 1980s and the 1990s, and the average mean length was 6.91 cm. In the 1980s, herring followed a similar pattern to cod, haddock, and capelin, but in the 1990s the pattern was almost the opposite to the pattern of cod and haddock.

Redfish had no trends in the mean lengths. There was little variation between the years and the average mean length was 3.80 cm.

3.3. Comparing to old indices

Comparing the Pennington estimator indices to the old area indices (Havforskningsinstituttet, 2003) the trends were similar (Fig. 4), except for capelin in 1980–1983, and for redfish in the 1980s. There was more dynamic in the series of Pennington estimators than in the area indices; the ratios between good and poor years were larger. The length correction of cod and haddock decreased this ratio.

Compared to the logarithmic indices (Havforskningsinstituttet, 2003) the trends were again similar (Fig. 5), but the strong year-class of herring in 1983 was not as evident in the Pennington estimator.

4. Discussion

The abundance indices estimated in this work show the large inter-annual variation in the 0-group abundance. Compared with the area indices, although the trends are similar, it is evident that the new methods retain more of the dynamics in the 0-group recruitment. There is not much difference between the results of the stratified mean estimator and the Pennington estimator for this particular survey. Both length and abundance estimates are influenced by the poor catching efficiency of the trawl for the smaller-sized cod and haddock, as shown by Godø et al. (1993) and Hylen et al. (1995).
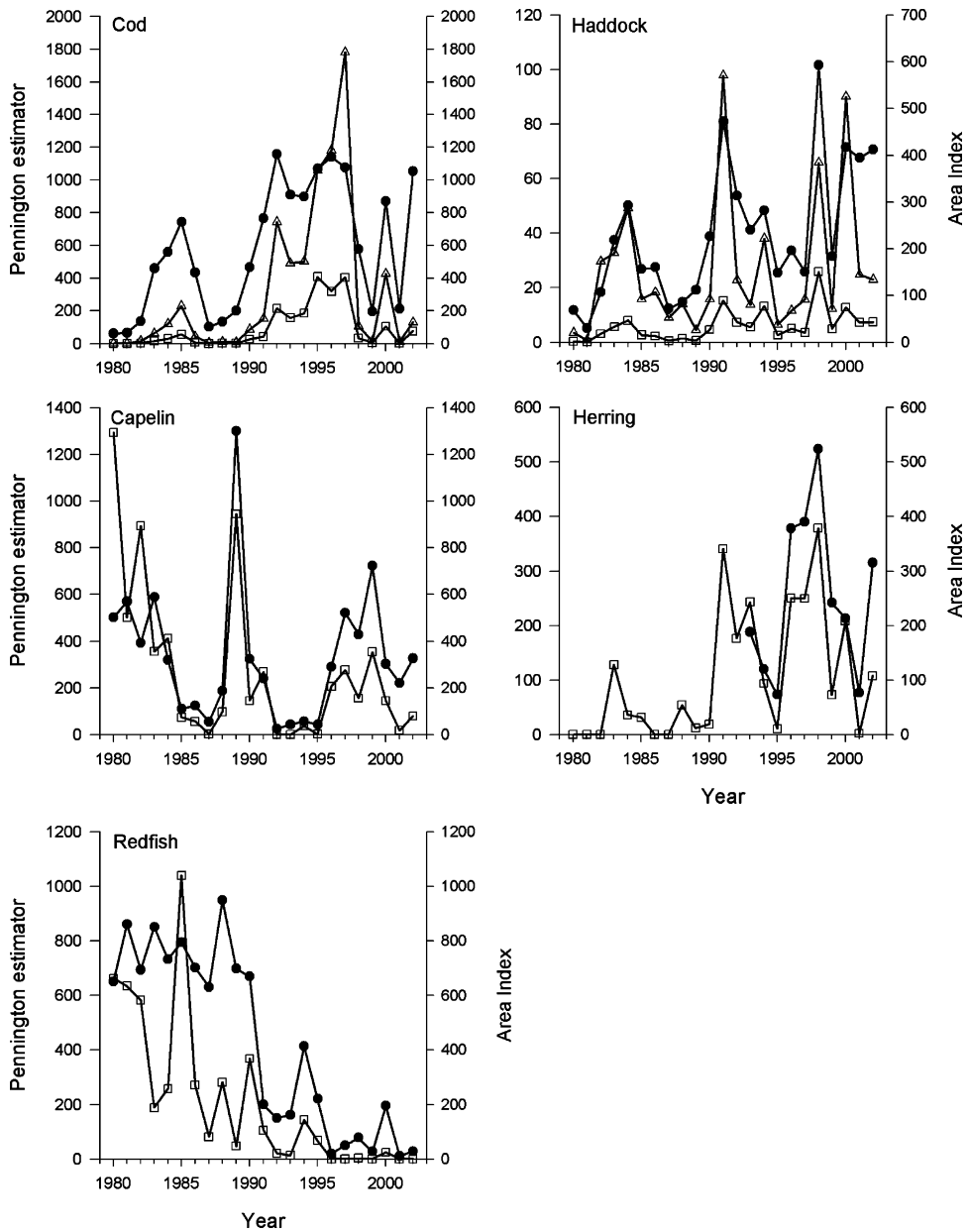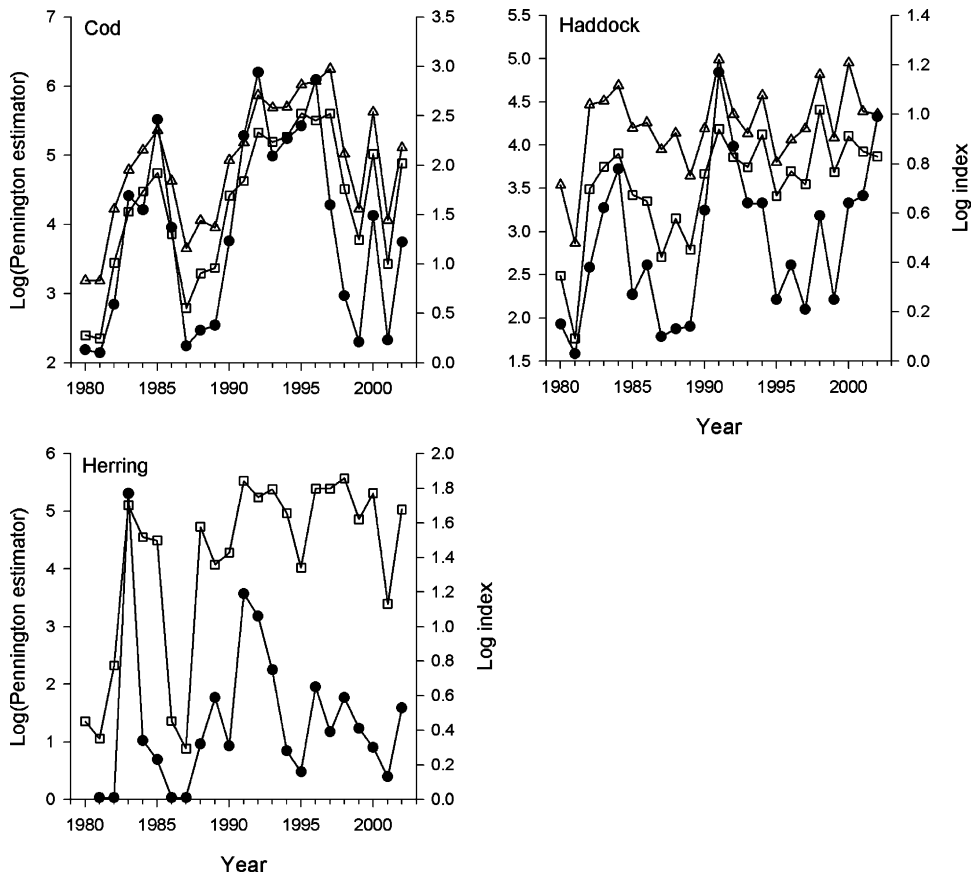
Fig. 4. Pennington mean estimators (open squares: without length correction, open triangles: with length correction) compared with area indices (filled circles).

This is a variable bias that increases with decreasing fish size, and there is reason to assume that this is a problem concerning the other fish species as well.

The data used in this work are gathered from the survey-database at the Institute of Marine Research,

Bergen. Until a few years ago, these data were punched manually from the original sampling forms, and even though a lot of effort has been put into quality checking the database, punching errors still occur frequently in the data. In later years, better sampling software that

Fig. 5. The log of Pennington mean estimators (open squares: without length correction, open triangles: with length correction) compared with logarithmic indices (filled circles).

test the data for errors as well as the introduction of electronic measurement boards and weights, with direct input to the software, have dramatically reduced the chance of punching errors. Another problem with the IMR database is the lack of data prior to 1980 and Russian 0-group data in 1982 and 1984.

The 0-group survey has been fairly consistent since 1985 with regards to trawling procedure and the standardized sampling trawl, but the distribution of trawl stations and the coverage of the survey area have varied from year to year. Differences in the distance between trawl stations can influence the standard errors of the estimated mean densities. More important, it can affect the mean estimates if the distances vary within a stratum. For example, if the stations are closer together in an area with high fish-density than in areas with lower

fish-densities, the mean density will be overestimated. Through the period 1980–2002 there is a trend of better coverage of stratum IV and poorer coverage of stratum I and III. This change of coverage may have a negative effect on the index of redfish, because dense concentrations of redfish were found in the southwestern part of stratum I and in the western part of stratum III in the 1980s and these areas were not covered as well in the 1990s and in 2000–2002. The increased coverage of stratum IV has resulted in better coverage of the capelin distribution and may have a positive effect on the capelin index. The distribution of cod, haddock, and herring seems to be fairly well covered regardless of the change in area coverage, but the lack of Russian data in 1982 and 1984 affects all estimates for those years.

One possible source of error that is often assumed to be insignificant, but which there is not sufficient knowledge about, is the settlement of northeast Arctic cod and haddock. There is very little information in the literature about when cod and haddock in the Barents Sea change from a pelagic life-stage to a demersal life-stage. It is assumed that this transition occurs from late September to October for cod and gradually throughout the autumn for haddock (Bergstad et al., 1987). Reviewing some of the research performed on settlement of cod and haddock in other areas (Bowman, 1981; Koeller et al., 1986; Mahon and Neilson, 1987; Bolz and Lough, 1988; Lough and Potter, 1993; Salvanes et al., 1994; Tupper and Boutilier, 1995; Hussy et al., 2003), it is apparent that it is not possible to generalize about when or at which length settlement occurs. The timing and size at settlement of cod and haddock seems to be regulated by both biological and environmental factors where time of spawning, growth rate, food abundance, presence of predators and suitable habitats are important factors that may cause variation in settlement both within and between years. The mean lengths of cod and haddock estimated in this work suggest that the majority settle later in the autumn and at longer lengths than more southern stocks, but one cannot disregard that some fish may have settled at time of survey and that this bias may vary annually. This is clearly one problem that needs further investigation.

Drevetnyak (1995) reported that settlement of redfish *Sebastes mentella* takes place when they are 2 and 3 years old, but 0-group redfish may be distributed in the whole water column when strong year-classes occur.

Olsen and Soldal (1989) reported that although the year-classes of northeast Arctic cod were weak in 1987 and 1988, they found dense concentrations in shallow water along the Finnmark coast. Based on these and some earlier observations they argued that coastal 0-group cod recur every year and that its abundance is determined by the "holding capacity" of suitable habitat rather than by year-class strength. They estimated that in a year with a poor year-class of northeast Arctic cod, the coastal portion might be in the order of 10% of the total cohort. This coastal portion is not included in the abundance estimates and will amount to a serious negative bias in years with poor year-classes, but it will not have a large effect in years with strong year-classes.

The pelagic trawl has a fairly low catching efficiency for 0-group fish (30–40%), and the efficiency is posi-

tively correlated with fish density (Hylen et al., 1995). More efficient herding by otter-boards and sweep lines when there are high densities of fish can explain the difference in efficiency. This herding will positively bias the abundance indices because of the increased "mouth area", and because larger fish have better swimming capacity, they will be herded more efficiently and mean lengths may be over-estimated. The large-meshed netting herds the smaller fish insignificantly and they are lost through the meshes (Godø et al., 1993). This causes negative bias in the abundance indices and positive bias in the mean lengths. The low catching efficiency for small cod and haddock caused by the insufficient herding by the large-meshed netting is corrected for by Eqs. (3) and (4), but there are no available correction functions for other fish species. Godø et al. (1993) estimated that the fish needed to swim with a speed exceeding $38 \, \text{cm} \, \text{s}^{-1}$ for as long as 40 s to be herded into the cod-end, which is far greater than what can be expected of smaller 0-group fish. In addition, small fish are often seen to swim directly towards the meshes at various points along the net walls (Wardle, 1993), and 0-group capelin are often seen entangled in the large meshes of the trawl (own observations). Thus, it is reasonable to assume that there is also a selection of capelin, herring, and redfish and that this causes an annually varying bias in the estimated indices and mean lengths.

As discussed above the swimming capacity of the fish is important in trawl selection. Both fish length and temperature are important factors determining swimming speed and endurance of a fish. Larger fish can swim longer at the same speed or they can swim faster at the same endurance than smaller fish, and a reduction in temperature reduces swimming speed and endurance (He, 1993). Thus, in warmer years the trawl efficiency may be better than in colder years. This and the fact that trawl efficiency is better in high-density fish concentrations will cause the trawl selection to vary from year to year and between areas. Thus, the correction functions used in this work may not be appropriate in all circumstances. However, the gain in precision is likely greater than the bias that may be introduced by using them.

The decrease in the ratio of the best year to the worst year, which was found in the abundance indices of cod and haddock when length correction was applied, indicates that the bias caused by selection is larger when the year-classes are poor. This may partly explain the pos-

itive correlation between mean length and year-class strength for cod and haddock (Ottersen and Loeng, 2000). The correlation was also found in my study, but the correlation became weaker after length correction was applied. The more efficient herding of larger fish in high concentrations by the otter-boards and sweep lines may also contribute to this correlation.

The new set of abundance indices show, as expected, more of the dynamic in the 0-group recruitment than the area indices do. Although the results from stratified sample mean are similar to the Pennington estimator, the latter seems to be the preferable method for this particular survey because the estimates are more precise and the occasional large catches do not affect the estimates nearly as much as they do in case of the stratified sample mean (McConnaughey and Conquest, 1993; Pennington, 1996). Occasional large catches occur for all species throughout the time series and when they occur, the lognormal based estimate is normally smaller than the sample mean (Pennington, 1996). This can be seen in Table 2 where $\hat{\mu}_{st}$ is usually smaller than $\bar{y}_{st}$.

The lognormal based estimator of abundance has been criticized for not being robust when the model assumptions are violated (Myers and Pepin, 1990). The introduction of the cut-level k makes it possible to reduce the bias introduced by values close to zero and it is possible to adjust k such that the values above better fit a lognormal distribution, thus making the Pennington estimator more stable.

The estimated mean lengths show similarities between the species (Fig. 2) and indicate that there is a common factor that influences the length at this stage. Ottersen and Loeng (2000) showed that the length of 0-group cod, haddock, and herring is closely related to temperature. Cod, haddock, capelin, and herring have in general larger mean lengths in 1983–1984 and 1990–1992 than in 1986–1988 (Fig. 2). This coincides with warm and cold anomalies in the Barents Sea (Furevik, 2001) and supports the conclusion by Ottersen and Loeng (2000). Cod and haddock have very similar mean lengths after length correction (Fig. 3) and this is contradicting the previous hypothesis that haddock is on average larger than cod at this stage and that cod catches up the difference after it has settled. The results indicate that the difference in length previously seen in 0-group cod and haddock is caused by the selection properties of the trawl.

5. Conclusion

The goal of this work has been to improve the Barents Sea 0-group abundance indices of cod, haddock, capelin, herring, and redfish. Different sources of bias have been discussed and it is concluded that length dependent selection by the trawl is the most serious source of bias and it is recommended to apply the length correction functions in the estimates. Concern has been raised about early settlement as a source of bias for cod and haddock estimates. This seems to be negligible, but should be further investigated, although pelagic 1-group cod and haddock have been observed during the winter (Odd Nakken, personal communication). The Pennington estimator is concluded to be the most appropriate method of the two in this work. It is recommended that this method becomes the new standard for estimating 0-group abundance indices in the Barents Sea, and that the new time series are included in the future reports from the 0-group survey in the Barents Sea.

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Paper II

Density dependence and density independence during the early life stages of four large marine fish stocks

Density dependence and density independence during the early life stages of four large marine fish stocks

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Abstract

Recruitment variability caused by density-dependent and density-independent processes is an important area within the study of fish dynamics. These processes can exhibit nonlinearities and non-additive properties that may have profound dynamic effects. In this study we investigate the importance of spawning stock biomass (i.e., density dependence) and environmental forcing (i.e., density independence) on the age-0 and age-1 abundance of capelin (*Mallotus villosus*), northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring spawning herring (*Clupea harengus*) in the Barents Sea. We use statistical methods that explicitly account for nonlinearities and non-additive interactions between internal and external variables in the abundance of these two pre-recruitment stages. Our results indicate that cod, haddock, and herring experience higher density-dependent survival during their first five months of life than capelin. The abundance of age-0 cod depends on the mean age and biomass of the spawning stock, a result which has implications for the management of the entire cod stock. Temperature is another important factor regulating the abundance at age-0 and age-1 of all four species, except herring at age-1. Between age-0 and age-1, there is an attenuation of density-dependent survival for cod and herring, while haddock and capelin experience density dependence at high and low temperatures, respectively. Predation by sub-adult cod is important for both capelin and cod at age-1. We found strong indications for interactions among the studied species, pointing to the importance of viewing the problem of species recruitment variability as a community phenomenon, rather than as a population phenomenon.

Keywords: *Mallotus villosus*, *Gadus morhua*, *Melanogrammus eaglefinus*, *Clupea harengus*, Barents Sea, GAM, density dependence, density independence

Introduction

The annual variation in year-class strength within marine fish stocks has been an area of research that has historically received much attention (Hjort 1914, Frank and Leggett 1994, Rothschild 2000, Myers 2001). Recruitment variability of marine fish is large and has major biological and economic implications for the management of commercial fisheries. Thus, finding the causes of recruitment variability is a central challenge in fisheries ecology (Frank and Leggett 1994). Many factors have been found significant in the determination of year-class strength. These include maternal effects (Kjesbu et al. 1996, Solemdal 1997, Marshall et al. 1998, Marshall et al. 1999), spawning stock biomass (Fogarty et al. 2001, Myers 2001, MacKenzie et al. 2003), climatic conditions (Ellertsen et al. 1989, Hamre 1994, Ottersen and Sundby 1995, Planque and Fredou 1999, MacKenzie 2000, Ottersen and Loeng 2000, Sundby 2000, Dippner and Ottersen 2001, Ottersen and Stenseth 2001, Stenseth et al. 2002), zooplankton abundance (Cushing 1995, Beaugrand et al. 2003), density-dependent survival during egg and larval stages (Sundby et al. 1989, Myers and Cadigan 1993), predation, and cannibalism on juvenile fish (Bogstad et al. 1994, deBarros et al. 1998, Gjøsæter and Bogstad 1998).

Fish experience biological processes differently, through the different life-history stages; egg, larvae, juvenile, and adult. Rothschild (2000) stated the importance of considering each life stage as a specific component and suggested to use life-history theory as a framework for understanding and predicting the magnitude of compensation in populations. In this paper we investigate the importance of spawning stock biomass (SSB) and environment for the abundance of 0-group fish (4-5 months old) and the relationship between 0-group and age-1 of four major and commercially important fish species in the Barents Sea. Taking into account temperature, predation, cannibalism, average age of the maturing stock and average

spatial position, we adopt a comparative perspective to find similarities and differences between these species. In this respect our work has the strength of considering both density-dependent and density-independent sources of population variability in a stage-specific survival analysis. We use generalized additive models (GAM) and threshold GAMs (Ciannelli et al. 2004). The latter is a model approach where the shape of an explanatory function may change according to whether an external covariate is below or above a threshold value. Thus it is possible to include non-additive interactions in our analysis. By comparing the results from the fully additive models with the threshold formulations, we address not only the effect of intrinsic and extrinsic variables, but also whether the dynamics involved are additive, non-additive threshold or nonlinear.

Capelin (*Mallotus villosus*), northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring spawning herring (*Clupea harengus*) are four commercially important fish species in Norwegian waters, all using the Barents Sea as their nursery area (Fig. 1). All of these species spawn along the Norwegian coast, herring furthest to the south and capelin furthest to the north. Capelin spawns off the coast of Finnmark, northern Norway, and in some years off the Russian coast. Capelin eggs are demersal and the larvae rise to the surface after hatching and drift north and eastwards with the currents. 0-group capelin has a more north-eastern distribution than the other species, but may in case of spatial overlap be preyed upon and it is rare that capelin has a good year-class when cod, haddock, and herring are abundant. The presence of juvenile herring in the Barents Sea is shown to have a negative effect on survival of capelin (Hamre 1994, Gjøsæter and Bogstad 1998, Hjermann et al. 2004). Cod and haddock eggs and larvae drift northwards with the currents and into the Barents Sea. Herring has demersal eggs, the larvae rise to the surface after hatching and drift northwards by the Norwegian coastal current and eventually

into the Barents Sea. Strong year-classes of 0-group cod, haddock, and herring do often co-occur and the spatial distributions of these three species also overlap at the larvae and 0-group stage. Calanoid copepods are important prey to larvae and early juveniles of all species in this study (Helle 1994, Huse and Toresen 1996, Bromley et al. 1997, Gaard and Reinert 2002). Thus, it is possible that density dependence through inter- and intra-specific competition for food is present.
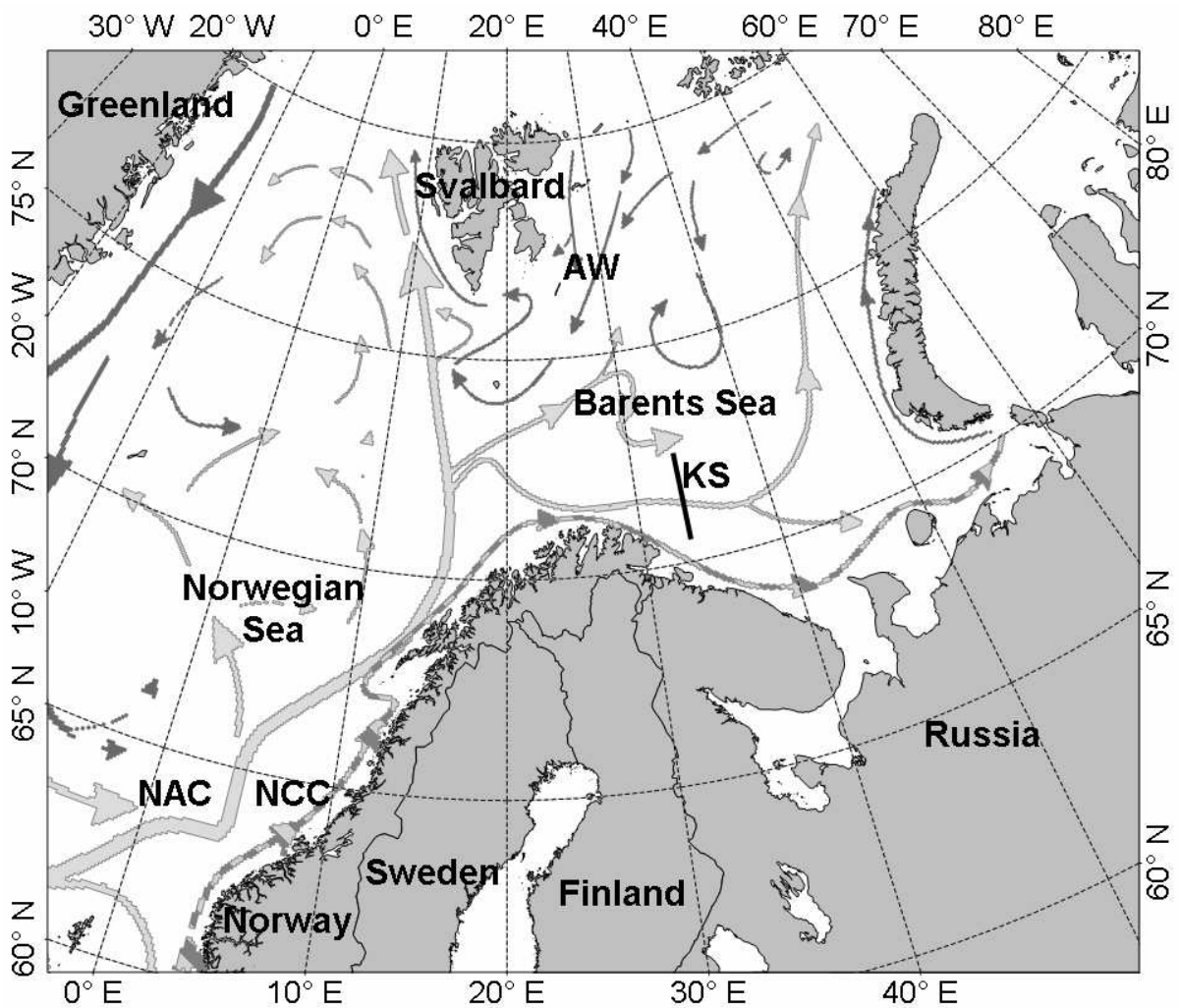
Figure 1 Norwegian Sea and Barents Sea with simplified current system. NAC stands for North Atlantic Current, NCC for Norwegian Coastal Current, AW for Arctic Water, and KS for the Kola section.

Methods

Density dependence is a fundamental concept in the study of fish population dynamics. Density-dependent processes can either be compensatory or depensatory (see e.g. Rose et al. 2001 for definitions). In this paper we will be referring to only compensatory processes when discussing density dependence, i.e. processes that promote a decrease of population growth at high densities. One or two mechanisms causing compensatory effects are generally assumed: (1) death as a direct effect of competition for limited resources, and (2) death as a secondary effect due to changes in growth rate, condition, susceptibility to predation, cannibalism and diseases (Frank and Leggett 1994). Compensatory density dependence is important in management because it acts to stabilize populations, but it is still an unresolved issue how to properly account for it (Rose et al. 2001). Evidence of strong density-dependent mortality within cohorts has been found for several fish species, and competition for food has been proposed as a possible density-dependent mechanism (Myers and Cadigan 1993). For example, Huse and Toresen (1996) concluded that 1-3 year old capelin and herring are potential competitors for food during early summer in the Barents Sea and that herring was more likely to win this competition. Another example of density-dependent mortality is the positive correlation found between occurrence of cod-cannibalism and abundance of 0-group cod (Bogstad et al. 1994). The main problems in including density dependence in management scenario are determining its actual magnitude (Fogarty et al. 1992, Rose et al. 2001), and its variation in response to density-independent factors. Often density-dependent and density-independent variables exhibit interactive (i.e., non-additive) effect on survival and recruitment (Ciannelli et al. 2004, Stenseth et al. 2004). It is important to be able to document nonlinearities and non-additive processes, since they may have profound dynamic effects (May 1976, Ciannelli et al. 2005). In our statistical models a nonsignificant

relationship between SSB and age-0 (or age-0 and age-1) indicates strong density dependence, while a positive and significant relationship may or may not indicate density dependence (depending on the slope).

The data

The variables used in the analysis of early life-stages abundances are listed in Table 1. Norway and Russia perform several annual fish surveys in the Barents Sea. During the last couple of years there has been a change in the organization of most of these. While earlier surveys were mostly carried out by only one of the countries targeting only a few species, most surveys today are carried out in collaboration between the Institute of Marine Research (IMR), Norway and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia, and are called ecosystem based surveys targeting several species in different trophic levels. We will in this work be referring to the old survey names, since the time series are named after these.

Capelin are measured acoustically in September-October. As well as age specific abundance indices, estimated biomasses of maturing fish are given, i.e. the biomass of capelin that will spawn the following year. Capelin catches are the natural logarithm of catches in numbers (10^9) of maturing capelin during fall and spring before spawning, capelin is assumed to be maturing when above 14 cm.

Table 1. List of variables used in the analysis of early life-stages abundances. Variables that were significantly affected by those listed in the first column are in bold in the third column (Modeled variables) and those that were not affected are in regular characters.

Variable	Definition	Modeled variables	Survey gear
Cap_{t-1}^{Mat}	Natural logarithm of maturing capelin stock biomass.	$\boldsymbol{Cap^0}$	Acoustic survey
$C_{t-1,t}^{Mcap}$	Natural logarithm of catch numbers of mature capelin.	$\boldsymbol{Cap^0}$	Fisheries statistics
Cap_t^0	Natural logarithm of capelin age-0 abundance.	$\boldsymbol{Cap^1}$	Pelagic trawl survey
L_t^{Cap0}	Mean length of capelin at age-0.	Cap^1	Pelagic trawl survey
Cap_{t+1}^1	Natural logarithm of capelin age-1 abundance.		Acoustic survey
Cod_t^{SSB}	Natural logarithm of cod spawning stock biomass.	$\boldsymbol{Cod^0}$	VPA estimate
Cod_t^{SSage}	Mean age in cod spawning stock.	$\boldsymbol{Cod^0}$	VPA estimate
Cod_t^0	Natural logarithm of cod age-0 abundance.	Cap^0, $\boldsymbol{Had^0}$, $\boldsymbol{Her^0}$, $\boldsymbol{Cod^1}$, Cap^1, $\boldsymbol{Her^1}$	Pelagic trawl survey
L_t^{Cod0}	Mean length of cod at age-0.	Cod^1	Pelagic trawl survey
Cod_{t+1}^1	Natural logarithm of cod age-1 abundance.		Bottom trawl survey
β_{trawl}	Catchability factor	$\boldsymbol{Cod^1}$, Had^1	Bottom trawl survey
Had_t^{SSB}	Natural logarithm of haddock spawning stock biomass.	$\boldsymbol{Had^0}$	VPA estimate
Had_t^{SSage}	Mean age in haddock spawning stock.	Had^0	VPA estimate
Had_t^0	Natural logarithm of haddock age-0 abundance.	$\boldsymbol{Had^1}$	Pelagic trawl survey
L_t^{Had0}	Mean length of haddock at age-0.	Had^1	Pelagic trawl survey
Had_{t+1}^1	Natural logarithm of haddock age-1 abundance.		Bottom trawl survey
Her_t^{SSB}	Natural logarithm of herring spawning stock biomass.	$\boldsymbol{Her^0}$	SeaStar estimate
Her_t^{SSage}	Mean age in herring spawning stock.	Her^0	SeaStar estimate
Her_t^0	Natural logarithm of herring age-0 abundance.	$\boldsymbol{Her^1}$	Pelagic trawl survey
L_t^{Her0}	Mean length of herring at age-0.	$\boldsymbol{Her^1}$	Pelagic trawl survey
Her_{t+1}^1	Natural logarithm of herring age-1 abundance.		Acoustic survey
CoG^N	Center of gravity in N-S direction of investigated species at age-0.	Cap^1, Cod^1, Had^1, Her^1	Pelagic trawl survey
CoG^E	Center of gravity in E-W direction of investigated species at age-0.	Cap^1, Cod^1, Had^1, Her^1	Pelagic trawl survey
P^C	Natural logarithm of number of cod at age 3-6.	$\boldsymbol{Cap^0}$, Cod^0, Had^0, Her^0, $\boldsymbol{Cap^1}$, $\boldsymbol{Cod^1}$, Had^1, Her^1	VPA estimate
P^H	Natural logarithm of number of herring at age 1-5.	Cap^0, Cap^1	Acoustic survey
T^W	Mean winter (Dec.-March) temperature (^{o}C) 0-200m at the Kola section.	$\boldsymbol{Cap^0}$, Cod^0, $\boldsymbol{Had^0}$, $\boldsymbol{Her^0}$, $\boldsymbol{Cap^1}$, $\boldsymbol{Cod^1}$, Had^1, Her^1	CTD-data
T^S	Mean summer (June-Aug.) temperature (^{o}C) 0-200m at the Kola section.	Cap^0, Cod^0, Had^0, Her^0	CTD-data

A combined acoustic and bottom trawl survey to obtain winter age specific abundance estimates of cod and haddock has been carried out in January-March (4-6 weeks) since 1981. Since 1993 the survey area has been extended to the north and east. A smaller meshed codend was introduced in 1994, which improved the catching efficiency for smaller sized fish. This was taken into account in the analysis. Age-1 cod and haddock abundance estimates are retrieved from the bottom trawl indices (ICES 2004a). The spawning stock biomasses (SSB) of cod and haddock and the numbers of cod age 3-6 are from the VPA estimates by the Arctic Fisheries Working Group (ICES 2004a).

Juvenile herring are measured acoustically in May-June since 1983 when distributed in the southern part of the Barents Sea. There were no measurements of the 1980, 1981, 1986, and 1987 year-classes, but it is assumed that these year-classes were absent from the Barents Sea since they recruited in such low numbers to the 0-group stage (Toresen et al. 1998). There was no survey in 2003 either. Estimates of herring abundance at age-1 and total juvenile herring abundance (age 1-5) in the Barents Sea were retrieved from ICES (2004b) and supplied with information from Toresen et al. (1998). Herring SSB estimates are from the SeaStar assessment by the Northern Pelagic and Blue Whiting Fisheries Working Group (ICES 2004b). The weighted mean age in cod, haddock, and herring spawning stocks were estimated with spawning stock biomasses at age as weights.

An international 0-group survey has been carried out in the Barents Sea in August-September since 1965. The trawling procedure changed in 1980-1981 and the mid-water sampling trawl was standardized in the early 1980s. Thus, the execution of this survey has been fairly consistent since 1985. The trawl data back to 1980 was reviewed by Dingsør (2005) and a new set of abundance indices were established in collaboration with Russian

8

scientists and published in a joint survey report (Table 2.3 in Anon. 2005). All estimates concerning 0-group fish used in this work are based on the reviewed data. The age-0 center of gravity in the north-south direction (CoG^N) was estimated by weighted mean latitude where the age-0 densities at each station were used as weights. CoG^E is the weighted mean longitude of age-0 distributions.

The temperature series used are average sea water temperature 0-200 m along the Kola section (70°30' N to 72° 30' N along 33° 30' E) during winter, December to March, and summer, June to August (Tereshchenko 1996 and PINRO, pers. comm.).

The models

In this study we investigated processes involved in the determination of year-class strength at the 0-group and age-1 stage of capelin, cod, haddock, and herring. These processes were investigated using the generalized additive model (GAM) in the R (version 2.0.1) package mgcv (Wood and Augustin 2002) and threshold GAM formulations. Threshold non-additive formulations were modeled with the use of tgam library for R by Kung-Sik Chan (Ciannelli et al. 2004).

Let X_t^a be the natural logarithm of the population abundance at life-history stage *a*, at time *t* and let $\mathbf{E}_t^j$ be a vector of environmental variables at time *t*, where the superscript *j* identifies the single components. Respectively, let *f* and g_j be nonparametric, smoothing functions specifying the effect of population abundance and environmental forcing on the population abundance at the following stage. Then the generalized additive formulations, for the age-0 and age-1 abundance become respectively:

$$X_t^0 = \alpha^0 + f(X_t^{SSB}) + \sum_j g_j(\mathbf{E}_t^j) + \varepsilon_t \tag{1}$$

$$X_{t+1}^1 = \alpha^1 + f(X_t^0) + \sum_j g_j(\mathbf{E}_{t+1}^j) + \varepsilon_{t+1} \tag{2}$$

The quantity α^a defines the average abundance at stage a and the term ε is random error assumed to be normally distributed. Note that we use the convention that functions with the same function symbol but different arguments are distinct. For example, $f(X_t^{SSB})$ and $f(X_t^0)$ are different functions.

In selection of the smoothing terms we applied a backward selection strategy. Where we started with a full model, containing all the variables examined, and removed one-at-a-time, starting with the least significant (highest p-value) until the generalized cross validation score (GCV, a measure of the leave-one-out mean squared error) was minimized (Wood and Augustin 2002).

The threshold non-additive formulation is composed by two additive formulations where the response changes according to an environmental force (e_t) above or below a threshold level r. The changes can be function switches from f_1 to f_2, $g_{1,j}$ to $g_{2,j}$, a switch in the intercept from α_1 to α_2, or a combination of these changes. Then the TGAM formulations become:

$$X_t^0 = \begin{cases} \alpha_1^0 + f_1(X_t^{SSB}) + \sum_j g_{1,j}(\mathbf{E}_t^j) + \varepsilon_t, & \text{if } e_t \leq r \\ \alpha_2^0 + f_2(X_t^{SSB}) + \sum_j g_{2,j}(\mathbf{E}_t^j) + \varepsilon_t, & \text{otherwise} \end{cases} \tag{3}$$

$$X_{t+1}^1 = \begin{cases} \alpha_1^1 + f_1(X_t^0) + \sum_j g_{1,j}(\mathbf{E}_{t+1}^j) + \varepsilon_{t+1}, & \text{if } e_{t+1} \leq r \\ \alpha_2^1 + f_2(X_t^0) + \sum_j g_{2,j}(\mathbf{E}_{t+1}^j) + \varepsilon_{t+1}, & \text{otherwise} \end{cases} \tag{4}$$

The threshold level (r) of the covariate e is chosen by minimizing the GCV score over the range of the covariate e. The procedure applied for the search of the threshold value is illustrated in Ciannelli et al. (2004).

Results

The final models of age-0 and age-1 abundance for the fully additive (GAM) formulations and the threshold (TGAM) formulations are given in Table 2 and 3, respectively. The best models were chosen according to the genuine cross-validatory squared prediction error (genuine CV, see Ciannelli et al. 2004 for details) and are further explained by plots of smoother functions (Figs. 2-9). In the age-0 abundance models there is no general trend to which model approach is better, while in the age-1 abundance models, the threshold formulations are better for three out of four species.

Table 2 Final formulations, adjusted R^2 (i.e. proportion of variance explained), and genuine cross validation (Genuine CV) of the best models for age-0 abundances.

Model	Formulations	R^2	Genuine CV
GAM	$Cap_t^0 = 10.175 + f_1(Cap_{t-1}^{Mat.}) + f_2(C_{t-1,t}^{Mcap}) + g_1(T_t^W) + g_2(P_t^C) + \varepsilon_t$	0.72	3.34
TGAM	$Cod_t^0 = f(Cod_t^{SSage}) + g(T_t^W) + \varepsilon_t + \begin{cases} 7.58, \text{if } Cod_t^{SSB} \leq 12.78 \\ 10.28, \text{if } Cod_t^{SSB} > 12.78 \end{cases}$	0.84	1.45
GAM	$Had_t^0 = 7.01 + f(Had_t^{SSB}) + g(Cod_t^0) + \varepsilon_t$	0.80	0.66
TGAM	$Her_t^0 = g(Cod_t^0) + \varepsilon_t + \begin{cases} 7.64 + f(Her_t^{SSB}), \text{if } T_t^W \leq 3.44 \\ 9.41, \text{if } T_t^W > 3.44 \end{cases}$	0.88	2.25

Age-0 abundance

The age-0 capelin model is unique because there is no direct estimate of the spawning biomass, at the time of reproduction (i.e., end of winter). The estimates of maturing capelin are given at October 1st and between this estimate and spawning the following winter, the

maturing stock is both predated on by cod and fished by commercial fishing vessels. It was thus necessary to include these factors in the models. For age-0 capelin, the GAM approach gave the best genuine CV value. As expected, both catches of maturing stock and predation by cod had negative effects, while the biomass of maturing stock had a positive effect (Fig. 2). Temperature had a dome-shaped effect with an optimum in the lower section of the temperature range. There was no significant effect of the presence of herring on the abundance of age-0 capelin.
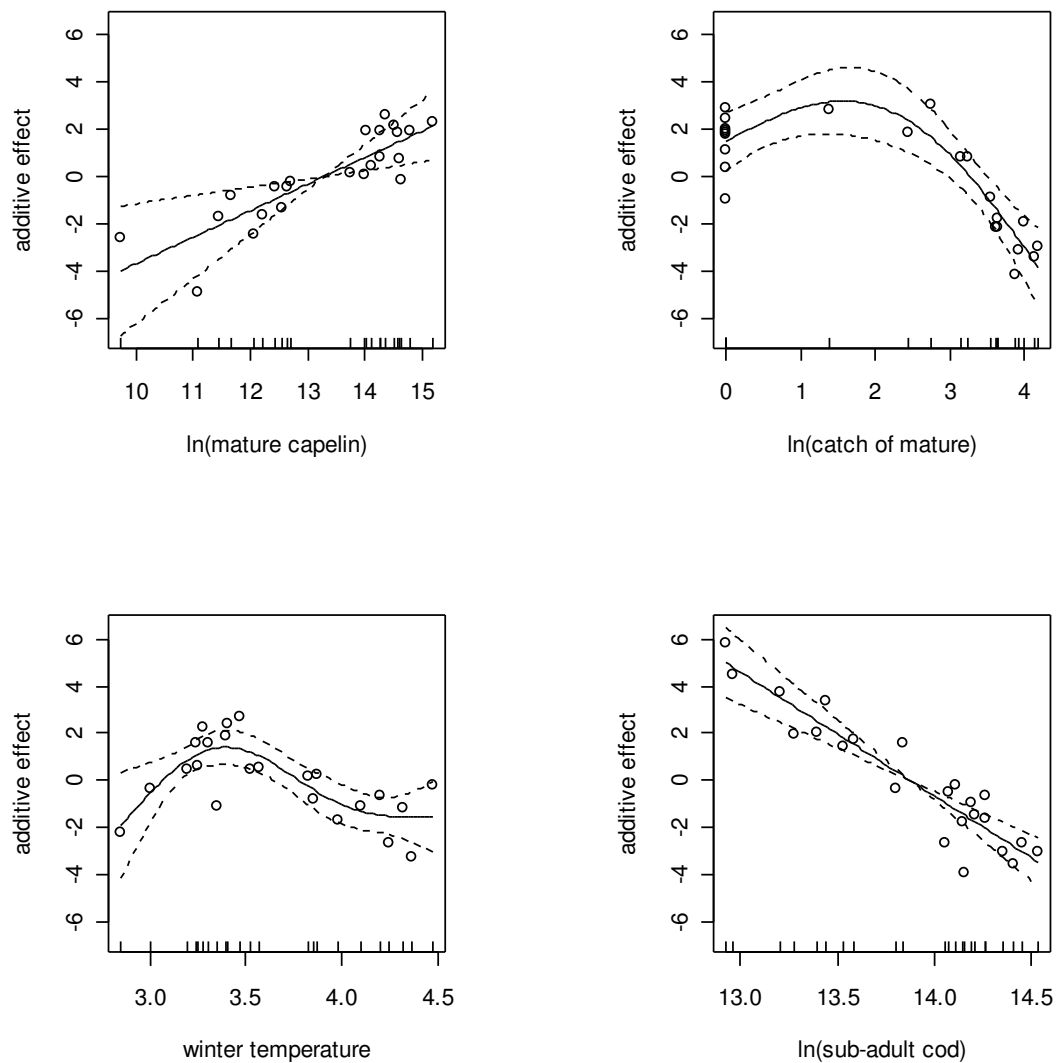
Figure 2 Factors affecting the abundance of capelin at age-0 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

Age-0 cod abundance was marginally better modeled by the TGAM formulation, where

spawning stock biomass had a significant (p<0.01) positive effect on the average abundance.

However, average spawning biomass was better modeled as a discrete effect (Table 2). The

mean age of spawning stock had a dome shaped effect with an optimum around 7.5 years

(Fig. 3). Temperature had a positive, asymptotic effect. The initially positive effect of

temperature indicates an increase of larval survival, probably due to increased food

availability during warm regimes. However, the subsequent plateau of the temperature effect

may indicate an increase of density-dependent mortality during the larval stages, when these

are highly abundant.
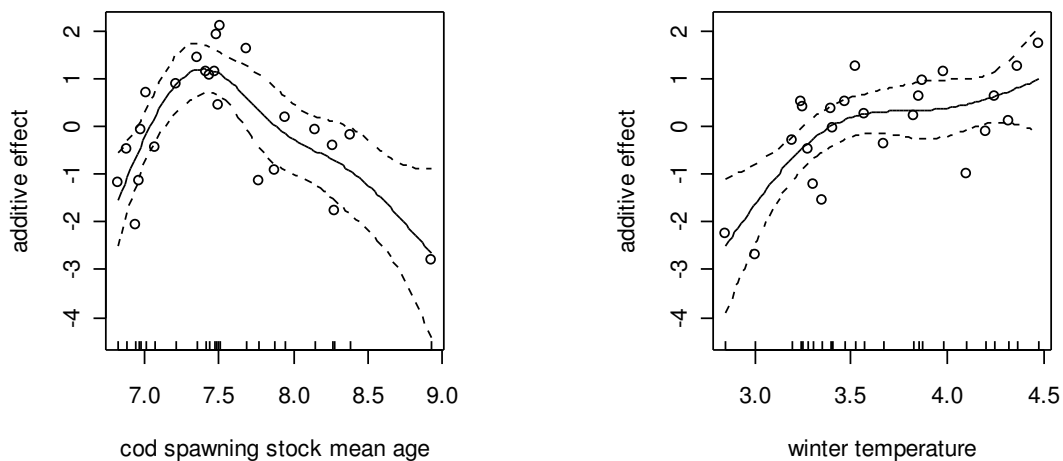
Figure 3 Factors affecting the abundance of cod at age-0 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

Both age-0 haddock and herring had similar responses to temperature as cod did. However,

when temperature was substituted by age-0 cod abundance, the haddock and herring models

gave better fit to the data and lower genuine CV values. These results suggest that there are

other underlying factors in addition to temperature that affect age-0 abundance of haddock

and herring. One possible explanation is availability of food. Higher temperatures leads to

increased production of zooplankton in the Barents Sea and more available zooplankton gives better survival of larvae and early juveniles of all three species. However, when the abundance of cod gets too high, the competition between species for food may increase and survival decrease (Fig. 4 and 5), i.e. density-dependent survival. The increased competition at high temperatures was also supported by the herring TGAM result which showed that spawning stock biomass was only important when temperature was low. However, the average herring age-0 abundance was higher at high temperatures (Table 2).
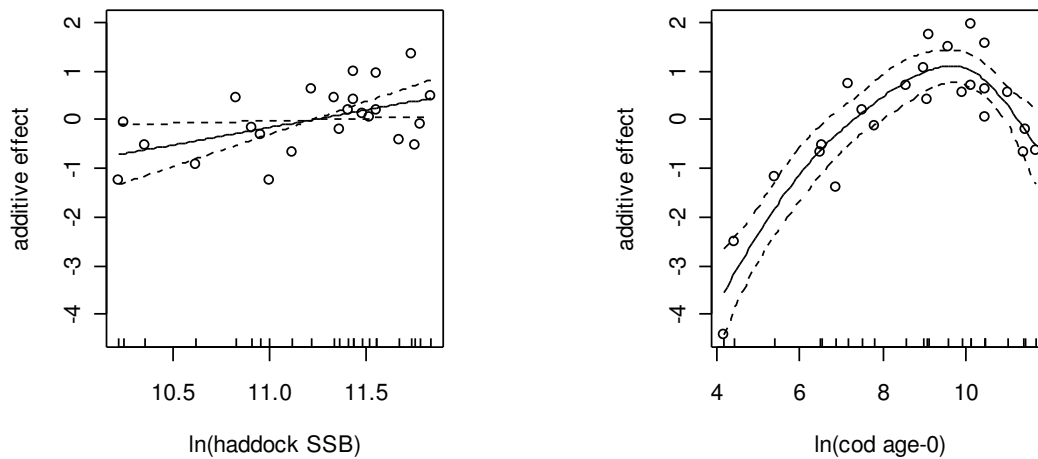
Figure 4 Factors affecting the abundance of haddock at age-0 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

14
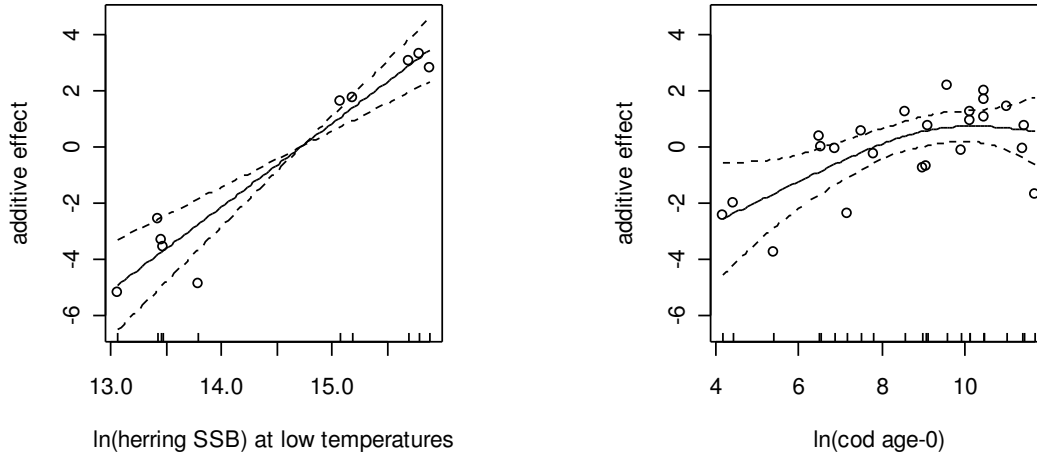
Figure 5 Factors affecting the abundance of herring at age-0 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

Table 3 Final formulations, adjusted R^2 (i.e. proportion of variance explained), and genuine cross validation (Genuine CV) of the best models for age-1 abundances.

Model	Formulations	R^2	Genuine CV
TGAM	$Cap_{t+1}^1 = 11.39 + g_1(P_{t+1}^C) + g_2(T_{t+1}^W) + \varepsilon_{t+1} + \begin{cases} , \text{if } T_{t+1}^W \le 3.40 \\ f(Cap_t^0), \text{if } T_{t+1}^W > 3.40 \end{cases}$	0.76	1.07
TGAM	$Cod_{t+1}^1 = \beta_{trawl} + f(Cod_t^0) + \varepsilon_{t+1} + \begin{cases} 2.76, \text{if } T_{t+1}^W \le 3.54, \beta_{trawl} = 1.50 \\ 3.66 + g(P_{t+1}^C), \text{if } T_{t+1}^W > 3.54 \end{cases}$	0.92	0.95
TGAM	$Had_{t+1}^1 = 6.67 + g(T_{t+1}^W) + \varepsilon_{t+1} + \begin{cases} f(Had_t^0), \text{if } T_{t+1}^W \le 3.72 \\ , \text{if } T_{t+1}^W > 3.72 \end{cases}$	0.93	0.96
GAM	$Her_{t+1}^1 = 6.46 + f_1(Her_t^0) + f_2(L_t^{Her0}) + g(Cod_t^0) + \varepsilon_{t+1}$	0.92	1.75

β_{trawl} is due to a change in survey gear in 1994

Age-1 abundance

Capelin age-0 abundance had a positive effect on the abundance at age-1 at high temperatures (Fig. 6), while at low temperatures age-0 abundance was nonsignificant. The temperature threshold level was at 3.4°C and below this level the overall temperature smoothing function showed a positive effect with decreasing temperatures. High abundance of sub-adult cod (age 3-6) had a negative effect on the survival of age-0 capelin.
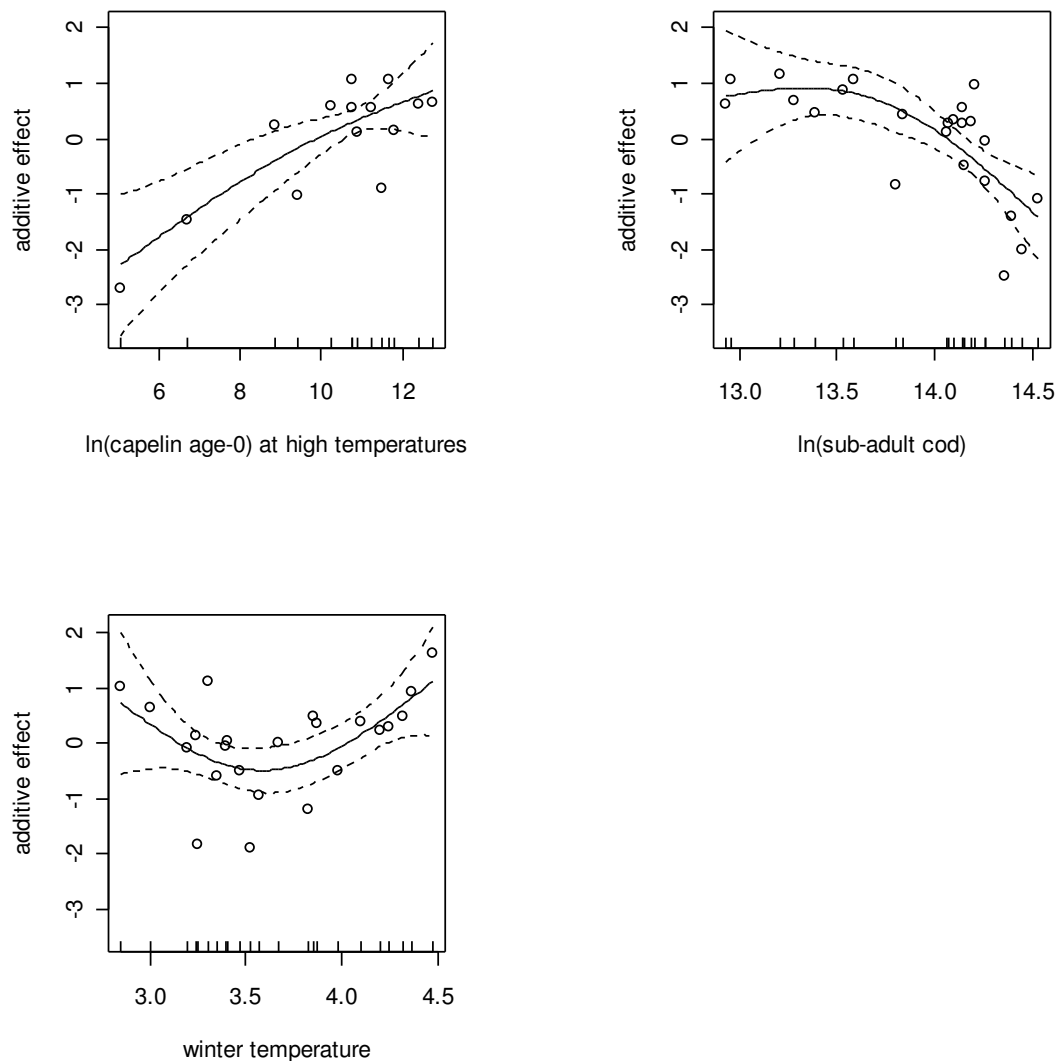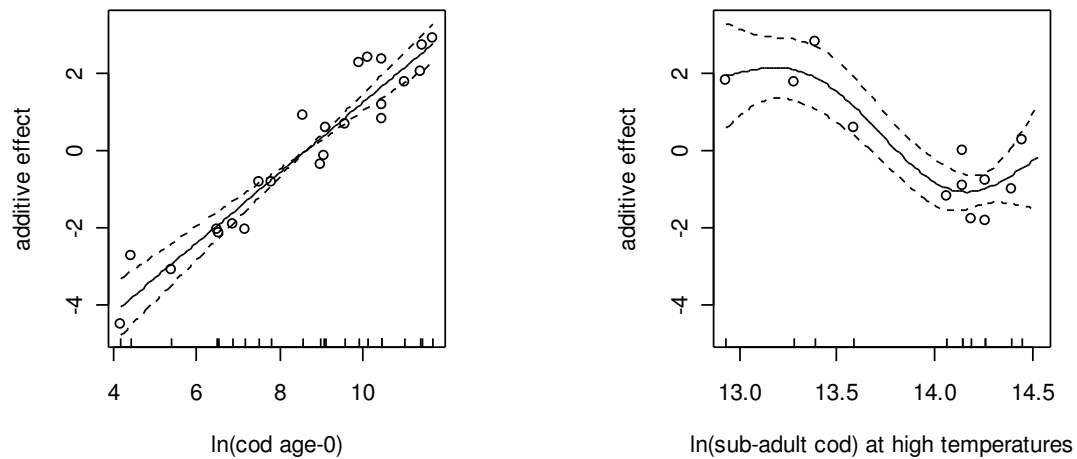
Figure 6 Factors affecting the abundance of capelin at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

In 1994 there was a change in the trawl gear used to survey age-1 cod and haddock. This change was included in the analysis as a categorical variable (1 and 2) distinguishing between the two trawl gears. For cod, this change resulted in an increase of age-1 abundance, indicating greater catch efficiency of the post-1994 gear. For haddock, the change in trawl gear showed no significant effect. Abundance of age-0 cod had a strong positive, linear effect on age-1 abundance (Fig. 7), indicating an attenuation of compensatory mechanisms on the survival of cod from age-0 to age-1. High temperatures had a positive effect on the

16

average abundance of age-1 cod. However, the non-additive model showed that cannibalism had a negative and nonlinear effect only during high temperature regimes, indicating an indirect negative effect of temperature.

Figure 7 Factors affecting the abundance of cod at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

The non-additive model for age-1 haddock abundance indicates density-dependent survival from age-0, where age-0 abundance only had an effect at low temperatures. Low temperatures had a negative effect on survival of haddock (Fig.8), while predation by sub-adult cod was not significant.

17
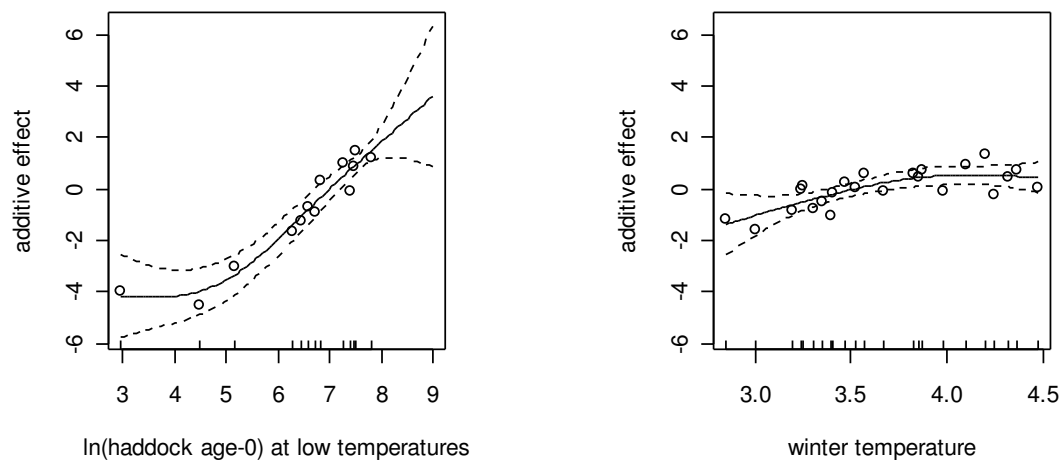
Figure 8 Factors affecting the abundance of haddock at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

Herring was the only species where length at age-0 had a positive effect. Longer fish resulted in better survival to age-1 (Fig.9). The monotone positive effect of age-0 herring abundance indicates an attenuation of density-dependent survival from age-0 to age-1. However, the negative effect of age-0 cod abundance indicates that there is competition between cod and herring.
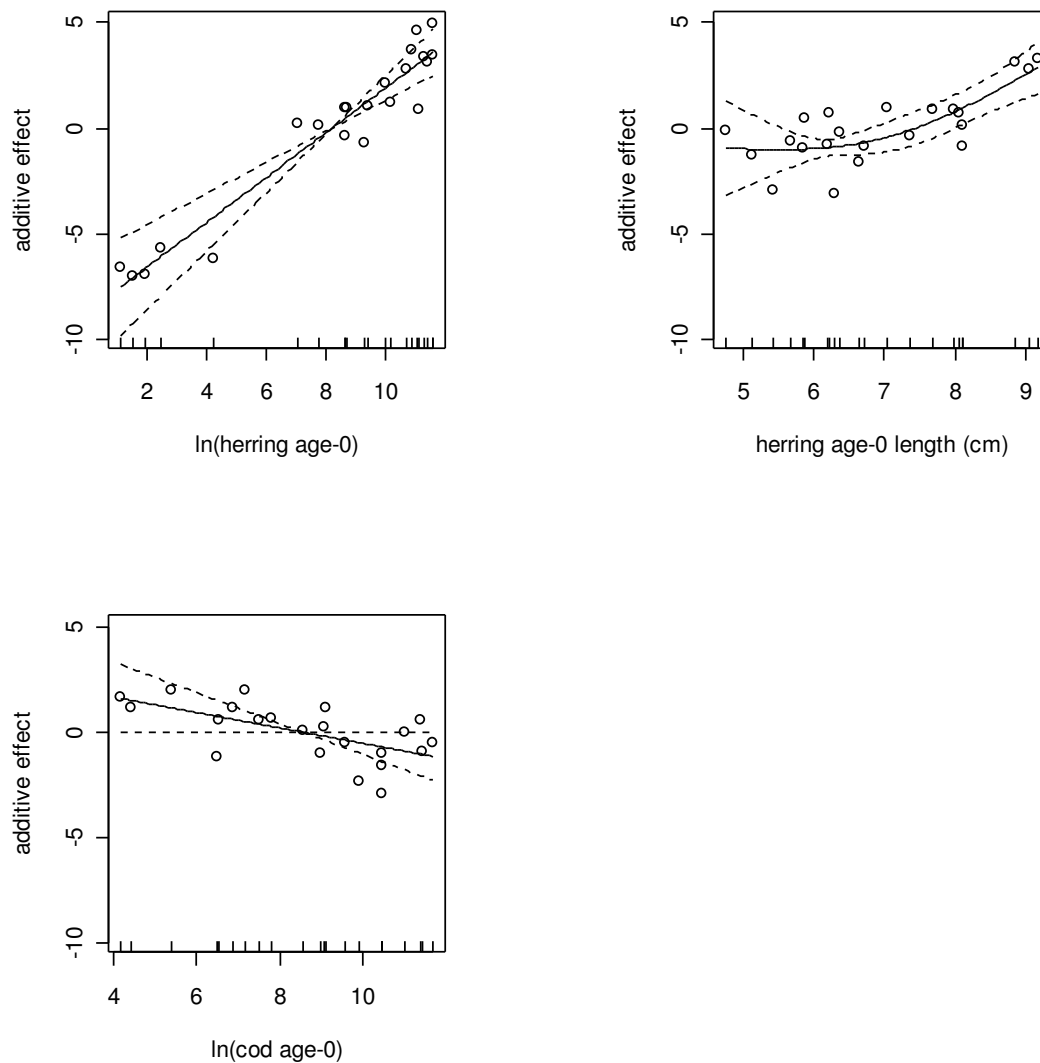
Figure 9 Factors affecting the abundance of herring at age-1 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

Discussion

We demonstrate that spawning stock biomass, temperature, and predation are important factors in determining year-class strength at the early life stages. Spawning stock biomass affect age-0 year-class strength for all species although to a varying degree and with different responses. Herring SSB only shows an effect when temperature is low, which

indicates that strong density-dependent mortality occurs at high temperatures. Cod SSB has a threshold effect at about 350 thousand tons; below this level the average abundance at age-0 is significantly lower than above it. This result confirms the importance of keeping the spawning stock at a certain level by management. Cod abundance at age-0 is also affected by the age composition of the spawning stock. Compared to first-time spawners, older cod arrive earlier on the spawning grounds, spawn over a longer time span, produce more eggs with a wider range of vertical distribution and lower mortality (see Solemdal 1997 for references). It is thus believed that a spawning stock with a higher mean age will produce more offspring. In northeast arctic cod there is a skewness in sex ratios at age of the spawning stock. The youngest age groups of mature fish are dominated by males because, on average, males mature approximately one year earlier than females (Ajiad et al. 1999). The older age groups are dominated by females, which might be caused by higher spawning mortality in males or a combined effect of earlier maturation in males and higher exploitation rates on mature than on immature fish (Jakobsen and Ajiad 1999). Thus the dome shaped effect of mean age in the spawning stock may be caused by a skewed sex ratio, at lower (domination of males) or higher (domination of females) extremes. These results have implications for management, highlighting the importance of maintaining a high diverse age-structure in the spawning stock. Similar conclusions were reached for the Islandic cod stock (Marteinsdottir and Thorarinsson 1998).

A relationship between temperature and recruitment has been shown by numerous studies and for several species (Ellertsen et al. 1989, Hamre 1994, Ottersen and Sundby 1995, Planque and Fredou 1999, MacKenzie 2000, Ottersen and Loeng 2000, Sundby 2000, Dippner and Ottersen 2001, Ottersen and Stenseth 2001, Stenseth et al. 2002). Increased growth and survival are influenced directly by temperature through increasing development

rates and indirectly through increased abundance of main prey (Sundby 2000, Ottersen and Stenseth 2001). Our results show that the link between temperature and age-0 abundance is lagged. Winter temperatures had a much stronger effect than summer temperatures. It is thus possible that temperature acts as a proxy for available food. However, it is also possible that temperature has a positive effect on the fecundity of the spawning stock, as previously shown in northeast arctic cod (Kjesbu et al. 1998). Ottersen and Loeng (2000) found a synchrony in year-class strength of cod, haddock, and herring in the Barents Sea and suggested that this was a result of mutual response to temperature fluctuations. Our findings support this conclusion, but in addition our results indicate that there is a competition for food between these species. Capelin has an optimal temperature effect at low temperatures, this in agreement with earlier findings suggesting that in cold years capelin uses the easterly spawning grounds, which is beneficial for avoiding predators (Hamre 1994).

While the temperature effect on age-0 abundance of cod, haddock, and herring was similar, the temperature effect on survival to age-1 was differing between these species. This difference may be caused by difference in behavior, as they grow. Temperature did not have a significant effect on herring survival. Age-0 herring is normally distributed high in the water column and show strong schooling behavior (deBarros et al. 1998). During the winter they are migrating towards the southern part of the sea where they are assessed as age-1 in May-June. This migration may cause the variation in ambient temperature to be different from the variation measured at the Kola section. Consequently, we are not able to find any relationship between temperature and abundance of age-1 herring. Cod and haddock start migrating towards the bottom gradually throughout the autumn (Bergstad et al. 1987). Temperature may influence the timing of settlement indirectly through increased abundance of food. If food is abundant in the pelagic they may choose to delay the migration towards

the bottom where the predators are located. Stomach investigations have shown that cod cannibalism is most prevalent where the smallest cod have been found in the bottom trawl (Bogstad et al. 1994), indicating that they are more vulnerable to predation and have a lower survival rate at the bottom than in the water column. Small cod and haddock also show strong diurnal variation in catchability in the winter bottom trawl survey because of vertical migration, and density of older cod is an important cofactor: the diurnal amplitude of small cod and haddock increased with increasing density of large cod, indicating anti-predator behavior (Hjellvik et al. 2004). This will cause the age-1 trawl estimates to be more negatively biased when the abundance of older cod is high and may partly explain the negative effect of sub-adult cod on age-1 cod. However, the stomach investigations (Bogstad et al. 1994) support our conclusion that cannibalism is an important factor affecting survival of cod to age-1.

The winter bottom trawl survey is often, and especially in cold years, restricted to the north and east by the ice border. The ice coverage is directly influenced by temperature, in turn also affecting the extent of the survey area. Thus in warm years the survey covers a larger area and age-1 cod are often found in dense concentrations in areas that are not sampled in colder years. This will contribute to the positive relationship found between temperature and cod abundance at age-1. Age-1 cod can be found in dense concentrations near the ice border and it is plausible that these concentrations continue underneath the ice. Additionally, age-0 cod are often found in areas covered by ice the following winter, and one and two year old cod tend to remain primarily in the areas where they settled during the end of their pelagic drift phase (Maslov 1960, Helle et al. 2002). Unlike cod, age-1 haddock are distributed further southwest than cod and the survey coverage of age-1 haddock is less influenced by the ice border. The problems with varying ice coverage and diurnal migration discussed

above demonstrates that the winter bottom trawl survey is not optimal for surveying age-1 cod abundance and thus caution is needed when drawing conclusions based on these data.

Larvae and age-0 fish of the studied species are distributed in the upper 40-60 m of the water column while cod and haddock age-1 are distributed closer to the bottom. In this respect, one may argue that the temperature series from the Kola section (0-200 m) is not the most representative for the water masses experienced by the studied fish. However, this time series has been shown to reflect the relative large-scale interannual variations very well (Dippner and Ottersen 2001).

In this study we found evidence of density dependence in the determination of year-class strength at age-0 for cod, haddock, and herring. It is difficult to draw conclusions on which density-dependent mechanisms are important based on the low resolution data we have. However, there are some explanations that are more plausible than others. Cod fecundity is positively correlated with the liver weight which is related to the abundance and quality of available prey (Marshall et al. 1999) - capelin being more suitable than young cod. Competition for food may lead to density-dependent reproduction, i.e. reduced fecundity, and modeling has shown that a shortage in food may result in an increase in the proportion of the mature stock that will skip spawning (Jørgensen et al. in press), amplifying this density-dependent effect. This also points to the danger of treating spawning stock biomass as an error-free independent variable in stock-recruitment analysis. Increased competition for food and increased predation at high densities, from species not included in the models, are other factors that will contribute to density dependence. For example in the southern Barents Sea, minke whale (*Balaenoptera acutorostrata*) switches from a diet of krill and capelin to a

diet of herring when herring produces strong year-classes and are abundant in the Barents Sea (Haug et al. 2002).

Our results indicate that capelin experience density-dependent survival to age-1 when temperatures are low. This may be related to the stronger year-classes of age-0 capelin and reduced prey production at low temperatures, i.e. increased competition. Haddock show density-dependent survival at high temperatures, which may be caused by increased competition from strong year-classes of cod and herring.

Previous studies have shown that the presence of herring in the Barents Sea has a negative effect on the capelin larvae (Hamre 1994, Gjøsæter and Bogstad 1998, Hjermann et al. 2004). Our results did not confirm these findings, but are more in agreement with the conclusion by Huse and Toresen (2000) who studied herring stomach contents during summer of 1992 and 1993. They confirmed that predation took place, but the observed rates were too low to explain the poor capelin recruitment. However, in the studied period the abundance of herring in the Barents Sea is positively correlated with both abundance of sub-adult cod and temperature, which are included in our capelin model. Thus we can not exclude the possibility that herring has a negative effect on capelin recruitment. We might have been able to confirm this effect if we had a direct estimate of capelin spawning stock and did not have to use the estimate of maturing stock. An estimate of either mean age or mean length would probably also improve our capelin age-0 model, because capelin fecundity is positively correlated with length (Gjøsæter 1998).

We have demonstrated how the intensity of density dependence can change over temporally distinct environmental phases and through different life-history stages. In management of

24

marine fish stocks it is important to have a mechanistic understanding of the interactions between external and internal variables determining the strength of a year-class. A change in the intensity of density dependence during early life stages may potentially affect the dynamics of the entire population (Coulson et al. 2001, Stenseth et al. 2004). Furthermore, density-independent factors may indirectly affect the dynamics of populations through changes in the intensity of density-dependent regulation. Our study also highlights the importance of looking at species interactions when analyzing recruitment variability. Collectively, these findings should improve our understanding of the Barents Sea ecosystem, and may enhance our ability to forecast a scenario for high and low temperature regimes.

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Paper III

Spatial anatomy of species survival rates: effects of predation and climate-driven environmental variability

Spatial anatomy of species survival rates: effects of predation and climate-driven environmental variability

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Abstract

Factors affecting species survival can change over both temporal and spatial scales. The majority of survival analyses focus on temporal scales. Consequently, there is a limited understanding of how species survival varies over space and, ultimately, how spatial variability in the environment affects the temporal dynamics of species abundance. Using a data case from the Barents Sea, we develop a new analytical technique to study the spatio-temporal variability of the survival of cod (*Gadus morhua*) through their first winter of life (from age-0 to age-1). This is a delicate phase of the cod pre-recruitment life, as individuals are confronted with a suite of survival challenges, including settlement, optimal pre-winter body condition and growth, and predation avoidance. Over the 20 years analyzed (1980-2004), we found that the region where age-0 cod experience lowest survival, i.e., directly north of the Norwegian coastline, coincided with the area of highest abundance of older cod, one of their main predators. Within this critical region, the survival of age-0 cod was negatively affected by their own density and by that of older cod. Water temperature – a climate-driven variable of the Barents Sea, also affected survival of age-0 cod, probably by varying spatial overlap with their predators. We found that during cold years, age-0 cod survival increased in the eastern and coldest portion of the examined area that was typically avoided by older conspecifics. Based on these results we propose that within the examined area, the spatial pattern of age-0 cod survival is primarily affected by top-down mechanisms and by predation-driven density dependence. Climate-related variables can strongly influence the spatial survival of age-0 cod by affecting their distribution and the overlap with predators.

Keywords: cod, Barents Sea, spatial survival, recruitment, climate, GAM, habitat quality, spatial management, *Gadus morhua*

Introduction

Statistical studies of population dynamics have primarily focused on temporal scales of variability. In such a context, annual estimates of cohort abundance or survival are correlated with average values of biotic and abiotic factors throughout the studied region (e.g., Quinn and Niebauer 1995, Megrey et al. 1995, Ciannelli et al. 2004, Hjermann et al. 2004). These studies continue to provide valuable insight on how internal (i.e., demographic) and external (i.e., environmental) sources of variability affect species dynamics over time (e.g., Bjørnstad and Grenfell 2001). However, the spatial variability of these same internal and external factors is also likely to locally affect individual survival (Kareiva 1990, Tilman et al. 1997). It is also well established that species-environment interactions may be nonlinear (Stenseth et al. 2002, Dingsør et al. In review) and, thus, may be misrepresented when considered as an average over a spatial grid. It follows that an in-depth analysis of the factors affecting population survival over space (or more succinctly '*the spatial anatomy of species survival*') can ultimately elucidate the mechanisms that generate population variability over time. A common mechanism through which spatial dynamics can affect temporal variability of species survival is through spatial changes in overlap between predators and prey. For example, in a recent study on Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea shelf, Ciannelli and Bailey (2005) found that cod can quickly expand their distribution when thermal gateways across the shelf are present. This expansion causes an increased overlap between cod and one of their prey items – capelin (*Mallotus villosus*), and may result in a trophic cascade.

The conceivable spatial variability of species survival speaks to the need to understand its causes if we are to manage renewable resources within a spatial framework. Thus, the study

of spatial survival also bears important applied implications. However, species-environment relationships are complex due to their nonlinear and possibly nonadditive nature. An extreme case of nonlinearity over space may take the form of a threshold response, resulting in a drastic re-arrangement of species distribution following subtle changes of forcing variables. Threshold responses are common in species distribution data (Turner 2005), and may occur over contrasting climate regimes (Perry et al. 2005).

In this study we develop a new analytical technique that explicitly accounts for nonlinear and threshold responses, to study the spatial survival of juvenile cod (*Gadus morhua* L.) in the Barents Sea during a period of over 20 years (1980-2004). We focus on the survival of cod during the first autumn and winter of their life cycle. This is a delicate phase of cod pre-recruitment dynamics, as individuals are confronted with a suite of survival challenges, such as settlement in a favourable environment, optimal pre-winter body condition and growth, and predation avoidance. We believe that results from this and similar studies can elucidate the mechanisms involved in the generation of spatial and temporal variability of species distributions and survival. Such an understanding is sorely needed to better incorporate spatial considerations in the management of renewable resources.

The North-east Arctic (also known as Arcto-Norwegian or Barents Sea) cod is currently the largest cod stock on earth. In December-February, the majority of mature fish, typically from about six-seven years of age, migrate to the spawning grounds centered around the Vestfjorden and on the continental shelf outside Lofoten between 67°30N and 69°N (Fig. 1; Mehl et al. 1985). Spawning starts in early March, reaches maximum intensity during the first week of April and terminates by the first half of May (Ellertsen et al. 1989). The eggs, larvae and early juveniles drift north and northeastward carried by the Norwegian Coastal

Current and the Atlantic Current (Ellertsen et al. 1981, Bergstad et al. 1987). In late August and September the juvenile cod, now termed age-0, have drifted for 4–5 months. Just before settlement, from late September and onwards, their spatial extension reaches its maximum (Sundby et al. 1989), going from the coast of Spitsbergen to the central and eastern Barents Sea. One to two year old cod tend to remain mainly in the areas where they settled during the end of their pelagic drift phase (Maslov 1960, Helle et al. 2002). When they are large enough (aged three years or more) to feed on capelin, their preferred prey (Bogstad and Gjøsæter 2001), cod start to follow the capelin migration towards the coasts of Russia and northern Norway in winter, and north and eastwards during summer.
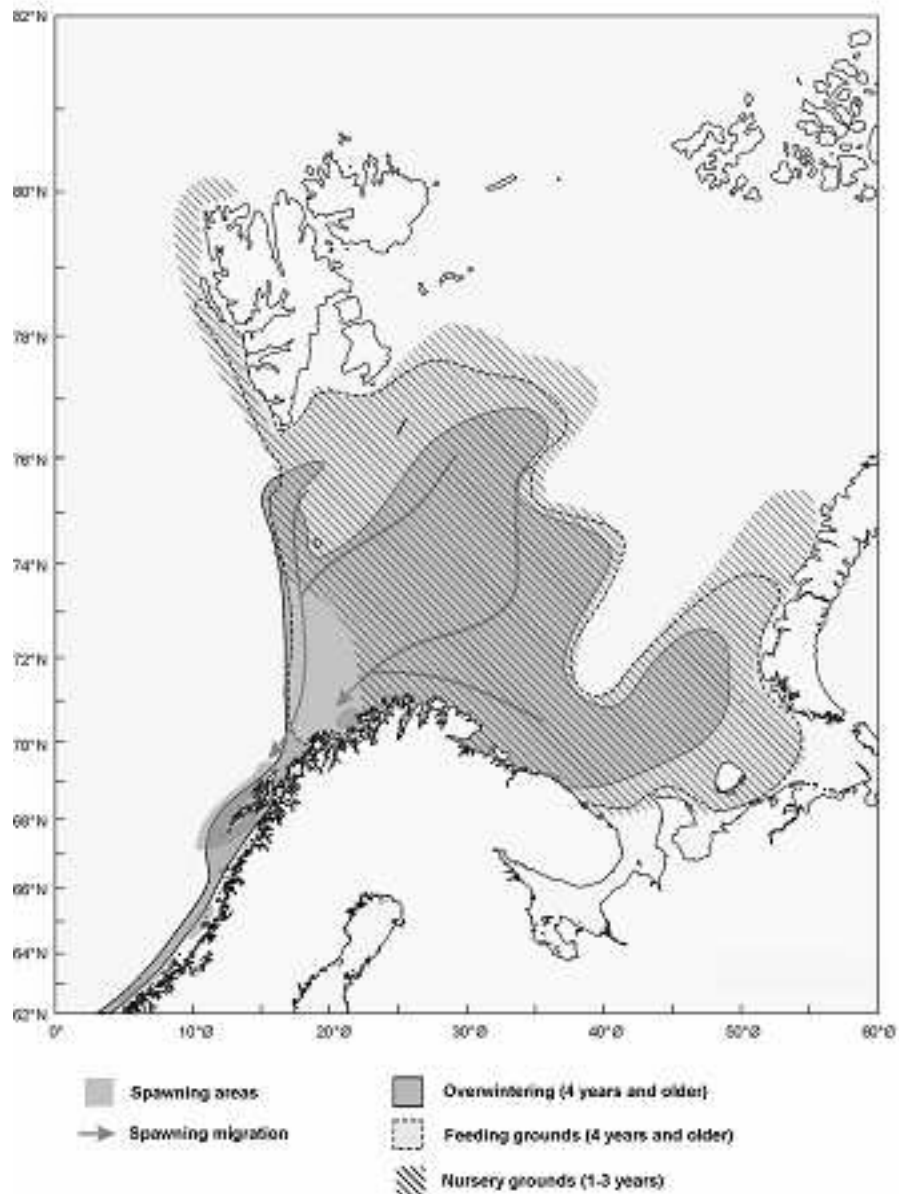
Figure 1 Spawning, overwintering, feeding and nursery areas for Northeast-arctic cod. The arrows indicate spawning migration patterns.

Methods

The data

The data used to estimate the survival metrics over space include the 1980-2004 age-0 cod catches from the August-September joint Norwegian-Russian midwater trawl survey (Anon. 2005, hereon referred to as 'fall survey'), and the 1981-2005 age-1 cod catches from the

February-March bottom trawl survey (Jakobsen et al. 1997, hereon referred to as 'winter survey'). Through these surveys, the same cohort is monitored twice within a period of about five months. Catches of older cod, larger than 35 cm in length, were also obtained from the winter survey. Both, age-0 and age-1 cod catches were standardized by effort, and expressed as number per nm^2 and number per nm trawled, respectively. Hereon, the standardized values of age-0 and age-1 catches will both be referred simply as 'catches', implying the procedure for the standardization.

Investigations of age-0 abundance in the Barents Sea have been carried out since 1965, but in a computerized format the data are only available from 1980. The sampling methodology also changed in the early 1980s (Dingsør 2005). Typically, smaller age-0 cod are under-represented in the catches, due to a gear selectivity issue. Thus, in our analysis, age-0 cod catches and body size were adjusted for gear catchability in relation to fish length (Anon. 2005). The numbers of age-1 individuals were isolated from the total bottom trawl catches based on age-length keys, varying by sampling sub-area and year surveyed. The length range of the age-1 class went from 5 to 24 cm, with most of the individuals being below 15 cm. In the swept area estimates of cod abundance from the winter survey, a length-dependent correction is applied in the calculations (Jakobsen et al. 1997). However, the correction factor only applies to individuals larger than 15 cm and there is no experimental basis for the correction factor of cod < 15 cm. Thus, we decided not to apply the length-dependent correction in our calculations of age 1 cod catches. After 1989 the bottom trawl was equipped with a rockhopper gear as opposed to a bobbin gear and we corrected the pre-1989 catches based on experimental work done at the time of the gear change (Godø and Sunnanå 1992). Moreover, after 1994 the net used in the bottom trawl survey was lined with smaller mesh (22 mm) codend, which significantly affected the catch of younger cod. To account for

6

this latter change in sampling methodology we included a gear factor in our models of spatial age-0 survival (see Methods: *Analysis of spatial patterns in age-0 cod survival*). Finally, age-1 cod catches were adjusted for diel variability (see Appendix A: *Adjustment for diel variability of age-1 cod catches*).

The co-located covariates used in the analyses of juvenile cod survival were water temperature (T), bottom depth (D) and time-corrected age-0 length (L_r). Water temperature was measured both during the fall survey (T_F), as the average of 0-50 m depth range (approximately the vertical distribution range of age-0 cod), and during the winter survey (T_W), at the bottom depth. Age-0 cod length increased by over 2 cm through the duration of the fall survey (Ciannelli pers obs). Thus, using the relationship between size and day of capture, we referred individual lengths to the median date of the fall survey.

Analysis of spatial patterns in age-0 cod survival

Prior to defining the spatial survival metrics, age-0 and age-1 cod catches, and co-located environmental covariates, were interpolated over a regular grid. The grid extent ranged from 68.0-76.8°N and 15.0-51.0°E, with increments of 0.8° and 1.8° in the latitude and longitude direction, respectively. The range and resolution of the grid matched those of the winter survey. At each grid point, age-0 and age-1 cod catches and the co-located covariates were derived as the average within a circle of radius (d) equal to 75% of the shortest distance between two grid points in the longitude direction. In establishing the length of d we tried to achieve a balance between the contrasting needs of reducing the overlap between two neighbouring circles (which would introduce an artificial autocorrelation in the data), and allowing for some movement of fish from the fall to the winter survey. Because of the

curvature of the earth, the value of *d* changed according to the latitude, and it ranged from 34.28 to 56.26 km at the highest and lowest latitudes, respectively.

Given two consecutive years, *t-1* and *t*, we calculated an index of spatial survival between the age-0 and the ensuing age-1 cod as follows:

$$S_{t,(\varphi,\lambda)} = \overline{x'_{t(\varphi,\lambda)}} - \overline{x_{(t-1)(\varphi,\lambda)}} \tag{1}$$

where $\overline{x'_t}$ and $\overline{x_{(t-1)}}$ are the natural logarithm of the average catch of diel-corrected age-1 and age-0 cod, respectively. φ and λ are degrees of longitude east and latitude north, respectively. Note that the so derived index is equally affected by both the actual local survival of age-0 cod and their movement rate. We assume that within the buffer area around each grid station, the index is mainly affected by survival. This is based on the notion that juvenile cod are rather sedentary once they settle (Maslov 1960, Helle et al. 2002). However, active movement prior to settling cannot be fully discarded, and its potential effect on our results will be further commented in the Discussion.

Survival indices of each grid station were regressed against co-located covariates using Generalized Additive Models (GAM). These are nonlinear and nonparametric regression techniques that do not require a-priori specification of the functional relationship between the dependent and independent variables (Hastie and Tibshirani 1990). We implemented two types of GAM formulations: (i) *additive*, where the effect of location (defined by latitude and longitude smoothers) on age-0 cod survival does not change from one year to the next, and (ii) *threshold*, where the effect of location changes in relation to external threshold variables. The additive formulation is:

$$S_{t,(\varphi,\lambda)} = k_g + s\ (\varphi,\lambda) + g_1(D_{(\varphi,\lambda)}) + g_2(T_{\ (\varphi,\lambda)}) + g_3(L_{r(\varphi,\lambda)}) + \varepsilon_{(\varphi,\lambda)} \tag{2}$$

8

where *s* and *g* respectively are two- (thin-plate regression spline; Wood 2003) and one-dimensional (natural cubic splines, Wood 2004) smoothing functions, *D* is the bottom depth, L_r is the time-corrected age-0 fish length, and *T* is water temperature, measured either in the fall survey (T_F) or in the winter survey (T_W). Fall and winter temperatures were correlated ($R^2 = 60.3\%$) and thus they were never simultaneously included in the same model, but either one or the other was selected. The quantity k_g is a constant indicating either of the two gear types used in the winter bottom trawl survey, i.e., before and after 1994, and $\varepsilon_{(\rho,\gamma)}$ is a normally distributed error term. Covariate selection strategy was based on the Generalized Cross Validation (GCV) – a measure of the model predictive squared error (Green and Silverman 1994).

In Eq. (2) the term $s(\varphi\ \lambda)$ captures the location effect, assumed to be constant from one year to the next. This formulation contrasts one in which the location effect on the age-0 cod survival, and the average survival level (*k*), are allowed to change according to the value of an external environmental variable (*E*). This additional feature of the analysis is essential to assess the nonlinear and possibly threshold effect of contrasting environmental and climatic regimes on the spatial distribution of juvenile cod survival. Specifically,

$$S_{t,(\varphi,\lambda)} = k_g + g_1(D_{(\varphi,\lambda)}) + g_2(T_{(\varphi,\lambda)}) + g_3(L_{r(\varphi,\lambda)}) + \varepsilon_{(\varphi,\lambda)} + \begin{cases} k_1 + s_1(\varphi,\lambda) & \text{if } E_t \le r \\ k_2 + s_2(\varphi,\lambda) & \text{if } E_t > r \end{cases} \quad (3)$$

The variable in *E* is a threshold covariate that partitions the effect of position over a 'low' or 'high' environmental regime. The threshold level (*r*) of the covariate *E*, separating the two regimes, was chosen by minimizing the GCV score among models that spanned the range of the covariate *E* (Ciannelli et al. 2004, Appendix B). In the Results and Discussion we will simply refer to 'low' or 'high' regimes of the examined threshold covariate, implying the existence of a reference point (*r*) separating the two regimes. We run five versions of the model in (3), each with a different threshold variable *E*, including:

(1) natural logarithm of the annual cod biomass (from age-3 onward, ICES 2005),

(2) natural logarithm of the annual harvest-corrected mature capelin biomass (Gjøsæter et al. 1998 for estimation methodology and ICES 2005 for values),

(3) natural logarithm of the annual average catch of age-0 cod (from the fall age-0 survey),

(4) the winter Arctic Oscillation (AO) index as an average of December to March monthly values (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml)

(5) the winter Barents Sea thermal index as an average from December to March of the 0-200m water temperature along the Kola section (Fig. 2; Tereshchenko 1996, values for later years kindly provided by PINRO, Murmansk).

Estimates of the mature capelin biomass refer to the end of September. Here, we have removed from the biomass estimates, the harvest from October to December. Each of the threshold variables was included in the analysis for its potential to affect the survival of age-0 cod, either directly via changes of predation intensity (related to the biomass of adult cod, and prey availability), or indirectly via changes in climate-driven environmental conditions (Arctic Oscillation and Kola water temperature).

Results

Average distribution of water temperature and cod catches

Both fall and winter water temperatures were on average highest toward the southwest end of the examined region. Fall temperatures sharply decreased northward and winter temperatures decreased northeastward (Fig. 2). Age-0 cod catches were highest in the central portion of the examined grid, from about 70 to 75 degrees north and from about 20 to 35 degrees east (Fig. 2). Catches sharply declined to the west, in correspondence of the shelf

break, and to the east, beyond 45° longitude. Age-1 cod catches were highest in the eastern

and northern portion of the grid, east of 35° of longitude and north of 73° of latitude, whereas

catches rapidly declined toward the westernmost edge of the grid and toward the shelf break

(Fig. 2). Peaks of older cod catches progressively shifted westward as the length of the

individuals increased (Fig. 3).
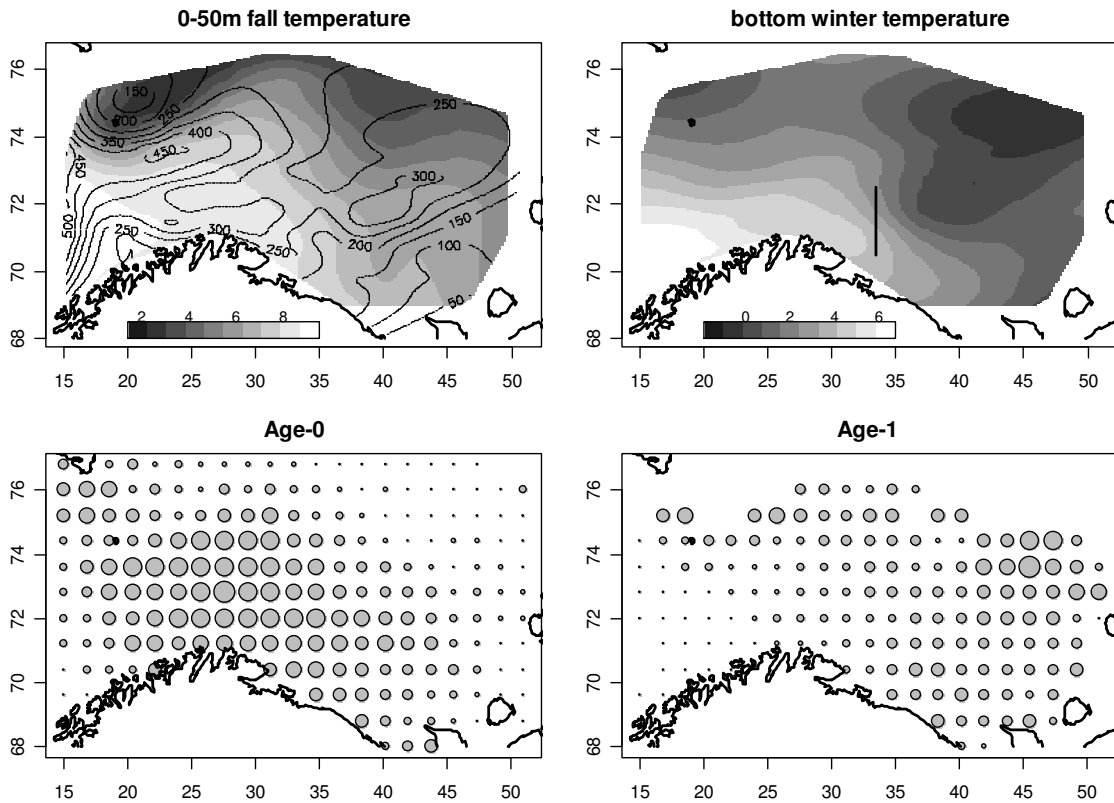
Figure 2 Average distribution of 0-50 m average fall water temperature (top left), winter bottom temperature (top right), age-0 (bottom left) and age-1 (bottom right) cod standardized catches. The area of the circles, in the lower two panels is proportional to the log-transformed and effort-standardized catches. Age-0 and fall temperature data include 1980-2004 fall surveys and age-1 and winter temperature data include 1981-2005 winter surveys. The depth contour and Kola section are also shown, in the top left and top right panels, respectively.
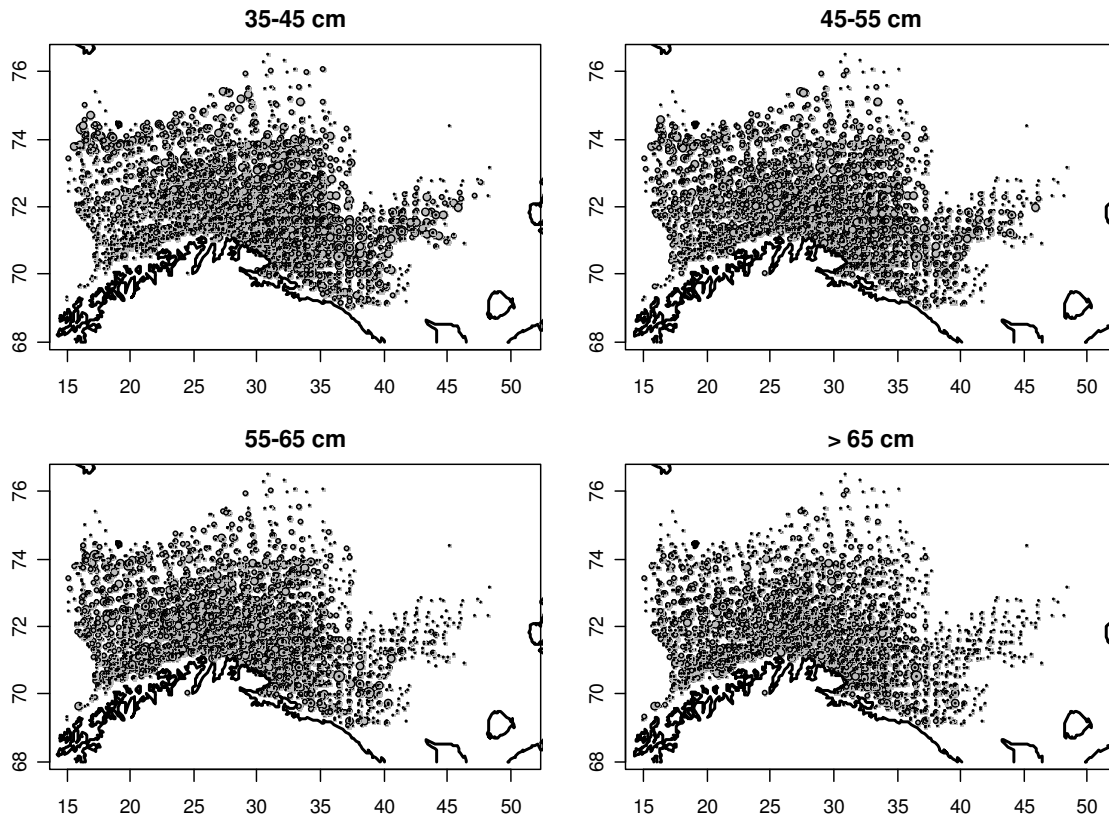
Figure 3 Average distribution of adult cod (1981-2005), during the winter survey, partitioned by size categories. The area of the circles is proportional to the log-transformed and effort-standardized catches.

Spatial survival of age-0 cod

Based on the predictions of the additive GAM formulation (Eq. 2), the area where age-0 cod experience the lowest survival (referred to as 'critical area') was bounded by the Norwegian coastline to the south, by 30° longitude to the east and by 74° latitude to the north (Fig. 4). Throughout the examined grid, age-0 survival was negatively correlated with bottom depth and water temperature, while the effect of length was U-shaped with a minimum at about 7-9 cm (Fig. 5).
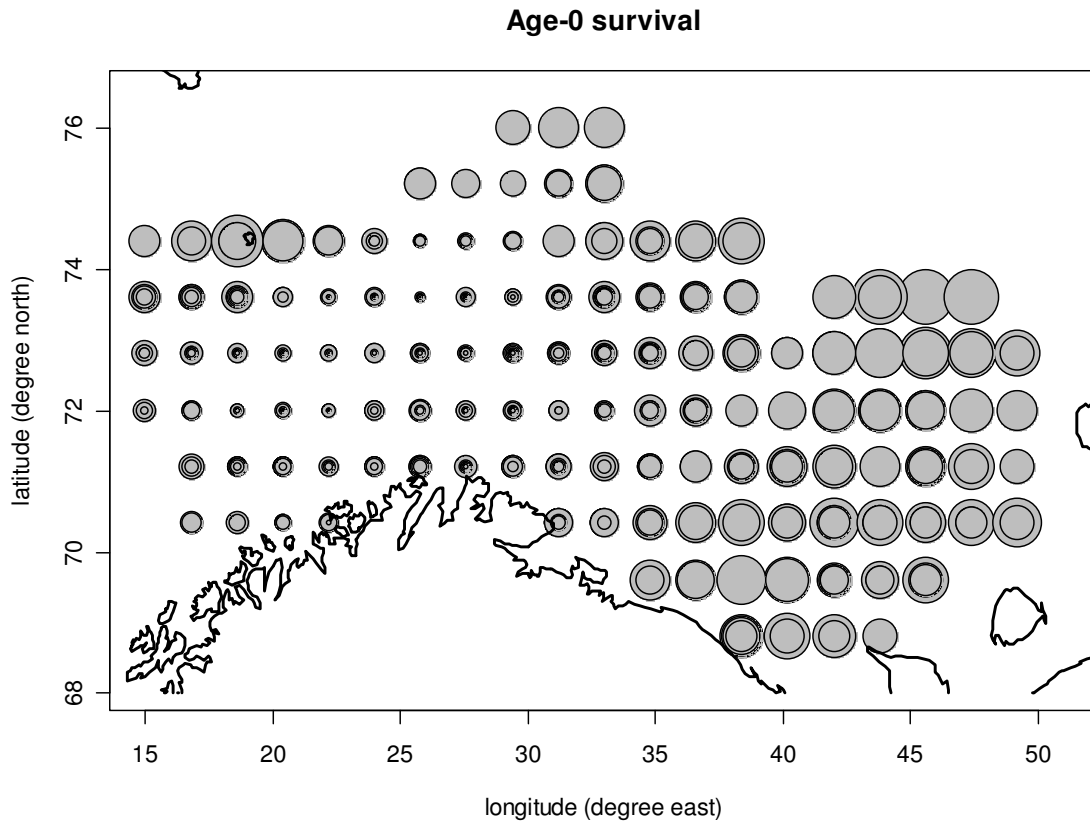
Age-0 survival

Figure 4 Spatial patterns of age-0 cod survival from 1980 to 2004 as predicted with an additive GAM model including geographic coordinates (latitude and longitude), bottom depth and winter temperature as covariate (see Eq. 2 in Methods). Circles are proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metric.
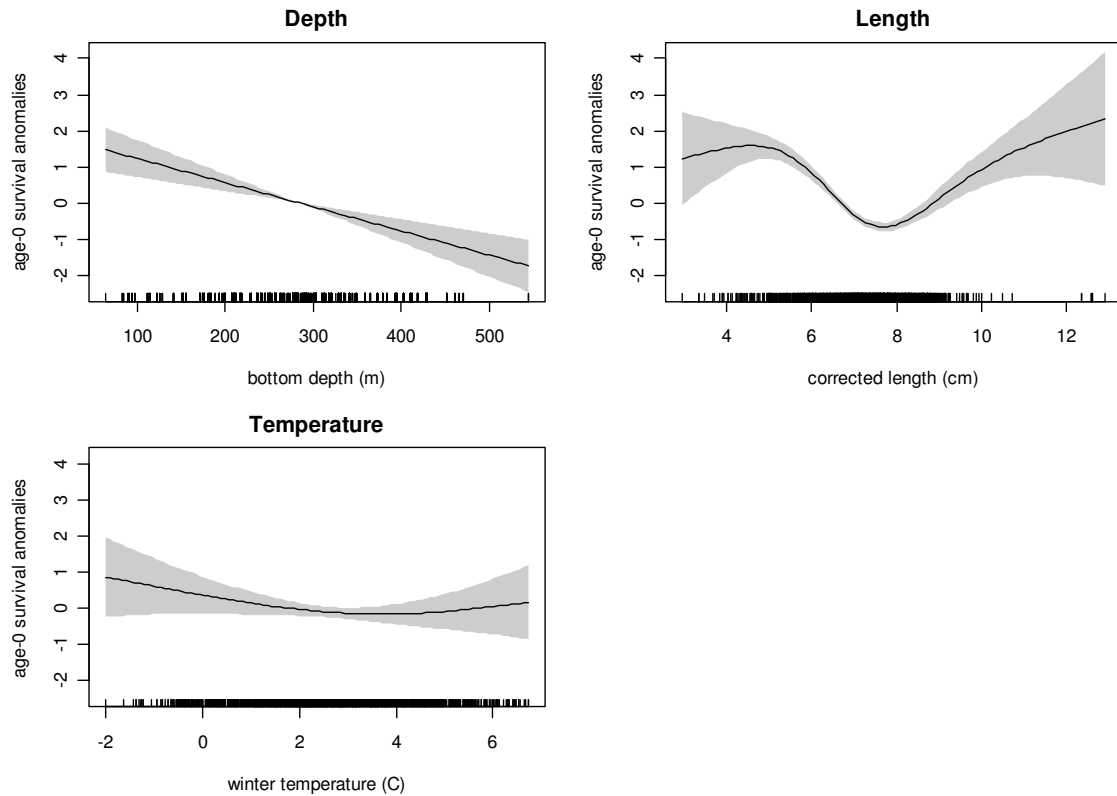
Figure 5 Effect of bottom depth, corrected age-0 length and winter bottom temperature on anomalies of age-0 cod survival, as predicted from the additive GAM model (see Eq. 2 in Methods). The shaded region indicates the 95% point-wise confidence interval and the rug along the x-axis indicate the location of the observations.
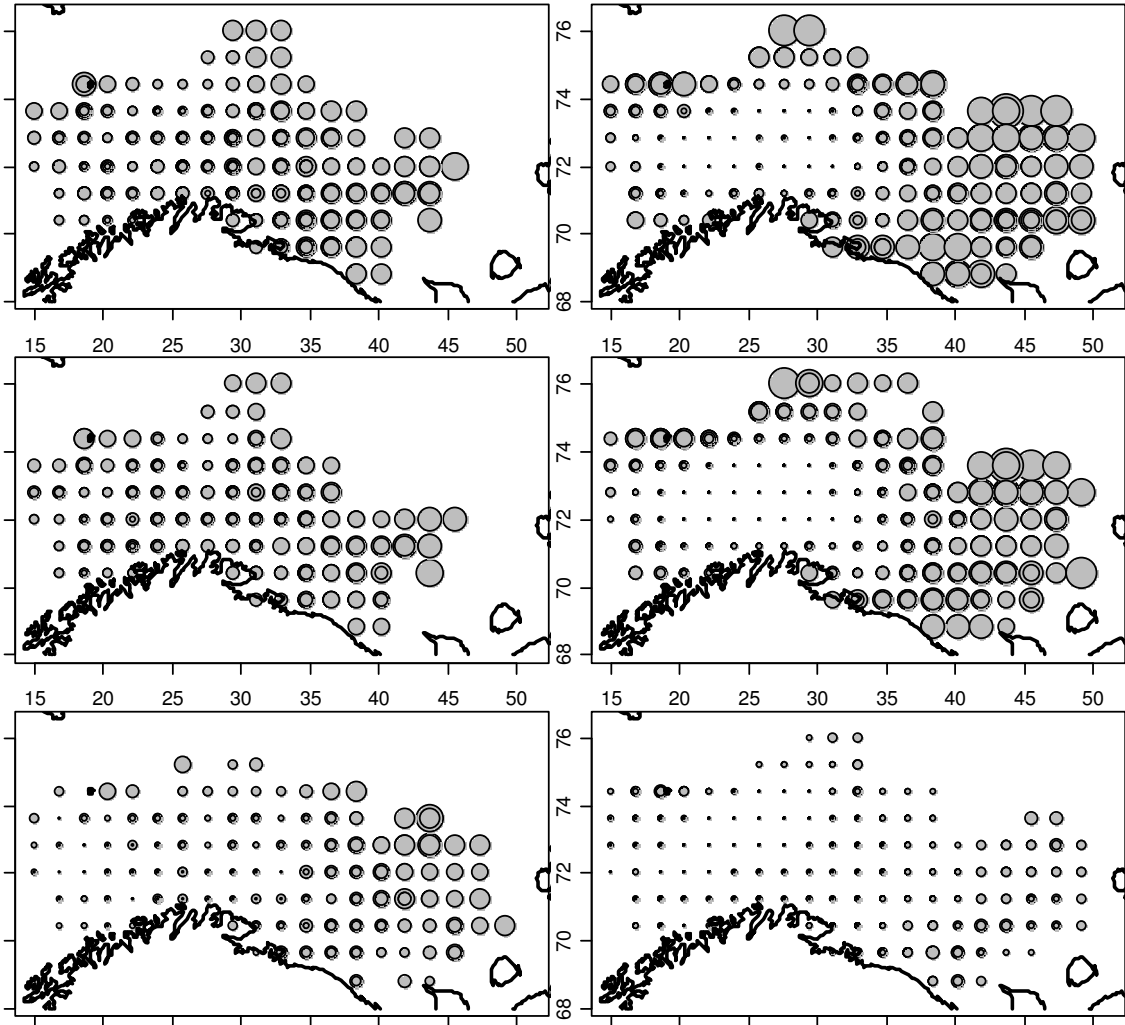
Results from the threshold GAM formulations (Eq. 3) clearly indicate that within the examined region age-0 cod survival exhibits a wide range of spatial and temporal variability, in turn linked with the background physical and biological regime of the environment. In particular, age-0 cod survival was considerably reduced throughout the critical area (Fig. 6) and as an average value throughout the sampled grid (Table 1) during years in which its own average biomass and that of adult cod were high (i.e., above the estimated threshold). The presence of high capelin biomass, the preferred prey of adult cod, did not visibly affect the pattern of age-0 cod survival (Fig. 6), and may actually cause a decrease of its overall average value (Table 1). Kola temperature and AO also affected the annual average and the spatial patterns of age-0 cod survival. During years in which Kola temperature was low, age-0 cod survival was on average higher, particularly in the easternmost end of the examined

region. AO affected the survival particularly in the central critical area, increasing during

high regimes (Fig. 7, Table 1). The estimated threshold values for each of the above

threshold models fell close to the median value of the covariate range, except for the capelin

and the AO models where the threshold value was closer to the lowest extreme (Appendix

B).

Table 1 Summary of the model results for each of the formulation examined. The coefficients K_1 and K_2 indicate the average value of age-0 cod survival throughout the inspected region during the low and high regime of the threshold variable, respectively. In all threshold formulations, the two coefficients (K_1 and K_2) were significantly different at 5% rejection probability. CV: genuine cross validation; Th(SD): estimated threshold value and standard deviation from cross-validation; Th-range: range of threshold variable in the analyzed time series; N: sample size.

Model type	R^2	CV	Th(SD)	Th-range	K_1	K_2	N
Additive	40.8	4.43	NA	NA	NA	NA	1407
Threshold – cod	46.1	4.08	13.96(0.01)	13.51-14.67	-7.32	-8.25	1428
Threshold – capelin	44.4	4.26	5.07(0.24)	2.83-8.27	-6.99	-7.81	1407
Threshold – age-0	47.2	3.96	11.33(0.06)	7.17-14.30	-7.16	-8.40	1407
Threshold – Kola temp	44.0	4.26	3.85(0.14)	2.85-4.47	-7.32	-8.04	1407
Threshold – AO	44.3	4.27	-0.51(0.39)	-1.40-2.39	-8.41	-7.59	1407

In all examined threshold GAM formulations, the effect of the other co-located modeled

covariates was similar to the one already described for the additive model (Fig. 5). Some

minor differences were found in the model with adult cod as a threshold variable, where

neither summer nor winter temperature caused a further reduction of the model GCV. In all

models, the effect of summer temperature on age-0 survival, when significant, was similar

(i.e., monotonic and negative) to the one shown for winter temperature in the additive

formulation (Fig. 5). From a visual assessment, none of the residual patterns from the

inspected models presented signs of heteroscedasticity or had strong departure from

normality.

Figure 6 Spatial patterns of age-0 cod survival as predicted from the threshold GAM formulations (Methods: Eq. 3). Horizontal pairs of plots show the model predictions during a low (left) and high (right) regime, as defined by the following threshold biological variables: age-3+ cod biomass (first row); age-0 cod from fall survey (second row); harvest-corrected biomass of mature capelin (third row).
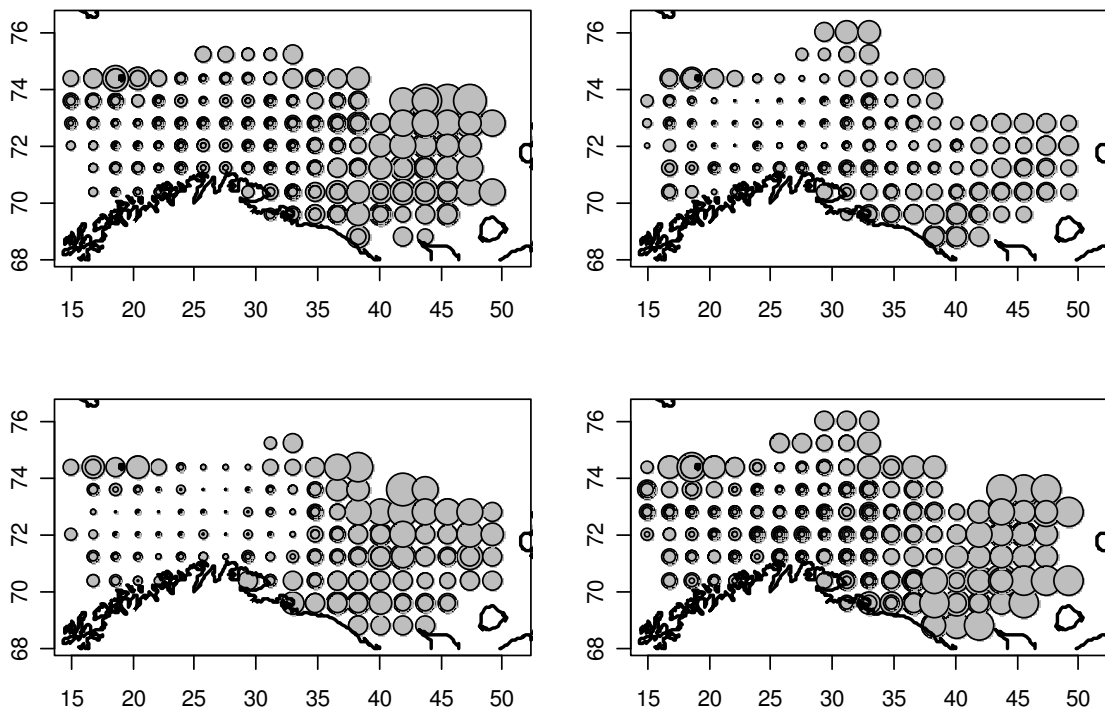
Figure 7 As in Fig. 6, for physical threshold variables. Threshold variables: winter Kola 0-200 m average water temperature (first row); Arctic Oscillation index (second row).

Discussion

Our analysis clearly indicates that the spatial pattern of age-0 cod survival undergoes significant interannual changes, in turn linked with the variability of co-located variables and with the background physical and biological regime of the Barents Sea. A noticeable reduction of survival was encountered during years with high adult cod abundance. The average abundance of age-0 cod also negatively affected its own survival. We believe that this was mostly the effect of increased cannibalism at high age-0 densities, perhaps due to a greater encounter rate, rather than the effect of resource limitation. In fact, similar negative effects on age-0 cod survival were also found when the ratio between age-0 and adult cod

average abundances was high, indicating that it was the relative availability of young cod rather than their absolute abundance, which caused the decrease in survival.

A number of studies support the importance of predation-driven effects on age-0 cod survival in the Barents Sea, however we are the first in showing their spatial impact. This additional information has allowed us to formulate more refined mechanisms on how age-0 and age-1 cod distribution and survival is regulated in the Barents Sea. Collectively, our results denote that within the examined grid, the spatial pattern of age-0 cod survival is strongly affected by top-down mechanisms. Internal control, in the form of predation-driven density dependence, may also be in place. In agreement with our findings, Bogstad et al. (1994) reported that the frequency of occurrence of cod cannibalism increases with the average abundance of juvenile cod. Also, the impact of predation on the spatial survival of juvenile individuals that we report here is further corroborated by the almost complete overlap that there is between the critical area of age-0 cod survival and the distribution range of older cod, particularly those larger than 50 cm.

The climate regime of the Barents Sea, here characterized by the AO index and by the Kola water temperature, also affected age-0 cod survival. The AO and the more commonly used North Atlantic Oscillation (NAO) index are highly correlated (Thompson and Wallace 1998), however the former is a better predictor for ecosystem effects of climate change in high-arctic systems (Aanes et al. 2002). A positive phase of the AO corresponds to a significant warming of the subsurface water in the Barents Sea as a result of increased inflow of Atlantic waters (Wang et al. 2004). During years of increased Atlantic inflow, age-0 cod distribution expands eastward due to greater and longer larval drift (Helle et al. 2002). On one side, such eastward shift in distribution co-occurs with increased food availability, and

may cause an increase of cod survival and growth through the first summer of life (Ottersen and Stenseth 2001, Ottersen et al. 2002). However, a more pronounced eastward distribution may also result in reduced growth at older cod stages, because young cod are forced to settle in the coldest region of the Barents Sea (Helle et al. 2002).

Other, so far unexplored, effects of climate and temperature may occur through variation of the spatial distribution and overlap between predator and prey. For example, in a recent analysis Dingsør et al. (in review) found a positive effect of Kola temperature on the abundance of age-0 cod – possibly the result of increased zooplankton availability during warm regimes. However, the same authors also found that when the winter Kola temperature was high, sub-adult cod (age-3 to age-6) had a negative effect on the abundance of the age-1 stage. Accordingly, in our analysis we found that during high Kola temperature years, age-0 cod survival was reduced particularly in the easternmost range of the examined region. A plausible explanation for these effects, is that older cod, which tend to reside in warmer waters compared to juveniles (Ottersen et al. 1998), may expand their distribution range to the east during warm years (Nakken and Raknes 1987), thus increasing the spatial overlap and consumption of the eastward displaced and newly settled juveniles.

The spatial pattern of age-0 cod survival was negatively correlated with co-located depth and water temperature, and nonlinearly correlated with age-0 length. We believe that the effect of depth was the consequence of active movement of age-0 cod prior to settling. Young cod may in fact migrate from deep toward shallow regions of the examined grid, to facilitate settling in favourable environments. In our analysis this effect would show as decrease of survival with increase of depth. However, once in shallow areas age-0 become more vulnerable to predation from older cod. The observed negative effect of co-located water

temperature on age-0 survival is in agreement with that of Kola temperature, and may also be a consequence of decreased cannibalism in cold waters. Typically, the preferred temperature range of older cod is considerably higher than that of juveniles (Ottersen et al. 1998), probably indicating a lower thermal tolerance of the former. Previous studies have in fact shown that juvenile cod can rapidly produce greater amount of antifreeze proteins compared to adults, and consequently can better and more quickly adapt to near-freezing temperatures (Goddard et al. 1997). Both fall 0-50 m and winter bottom water temperatures, decrease to the east and to the north of the examined grid (Fig. 2). This is also the region where age-0 cod experienced greater survival, which we believe was mostly due to the absence of adult cod in cold areas, rather than a direct effect of temperature on survival. It is also important to realize that the extent of the bottom trawl survey in winter is limited by the ice-edge. However, juvenile cod may still be abundant underneath the ice, where on one hand they may experience lower growth rates (Helle et al. 2002) but on the other hand they may find shelter from adult cod predation.

The effect of body length on survival was unexpected. It indicates that either very small or very large age-0 cod experience greater survival. The increase of survival at higher length extremes may be the result of size-selective mortality – a common mechanism in fish population dynamics (Sogard 1997). However, we see no easy explanation for the increase of survival at lower length extremes. One possibility is that in spite of the length-corrections applied to the age-0 catches and length estimates, smaller fish were still underrepresented in the fall survey.

Contrary to expectation we did not find a clear visible effect of capelin on the spatial pattern of age-0 cod survival. It is well-established that in the Barents Sea capelin are the most

important prey of immature (age 2-6) and adult cod (Bogstad and Mehl 1997, Bogstad and Gjøsæter 2001), and that capelin can affect adult cod survival and reproductive success (Marshall et al. 1998). However, the effect of capelin on the survival of juvenile cod is somewhat controversial. A plausible mechanism through which capelin affects juvenile cod survival is by releasing the latter from excessive cannibalism during high capelin years. Accordingly, some studies have found that the survival of juvenile cod increases when the ratio between adult cod and capelin abundance decreases (e.g., Hjermann et al. 2004). However, other studies have found no clear correlation between capelin abundance and cod cannibalism (Bogstad et al. 1994). Some of this apparent controversy, and the counter-intuitive capelin effect reported in our analysis, may be due to the seasonally variable nature of capelin distribution. Specifically, the peak of cod predation on capelin occurs during the end of winter and spring, when mature capelin must cross the gauntlet of cod predation to reach their spawning grounds in the northern coast of Norway and Russia (Gjøsæter 1998). The majority of the survival period considered in our analysis (September-February) falls outside of the alleged peak of cod consumption on capelin (January-June, Dolgov 2002), rendering the estimated age-0 cod survival independent from the availability of capelin. Also, the approaching route and landing site of capelin during their spawning migration is highly variable, and it is linked with the incumbent climate and thermal regimes of the Barents Sea (Gjøsæter 1998). In such circumstances capelin biomass may not necessarily be a good indicator of their availability to adult and sub-adult cod, unless other variables are also considered, such as climate indices and water temperature.

Our analysis presents several challenges, which to some degree may have affected the results. First, while the examined fall and winter surveys cover the areas where age-0 and age-1 cod abundances are highest, there are still large areas in winter that are covered by ice,

and that are not sampled. Consequently, there is the potential to miss important patterns of age-0 cod survival in non-surveyed areas. One of such areas may be west of Svalbard, which typically is densely populated by age-0 cod, but it is not surveyed in the winter. Second, in deriving the spatial survival between the age-0 and the age-1 stage we assumed a limited range of age-0 cod movement. Several studies have suggested that during their first two years of life juvenile cod tend to remain in the area where they settle at the end of the pelagic phase (Maslov 1960, Helle et al. 2002). Also, the extent of active movement that age-0 cod can perform within the periods that separate the two surveys (five months) is limited. However, sources of variation related to movement cannot be fully discarded from our analysis. For example, prior to settling age-0 cod may actively migrate toward shallow areas or away from the new forming ice. As already mentioned, of active migration toward shallower water may cause the reported negative effect of bottom depth on age-0 cod survival. The active migration toward ice-free areas may also explain why we predicted an increase of survival in the boundary and coldest regions of the surveyed winter areas. Third, part of the age-0 cohort will have settled before the survey, and therefore will be less vulnerable to the midwater sampling gear of the age-0 survey. How large this proportion is will vary interannually depending on sea temperature, which affects growth rates as well. Settlement time is likely to also differ geographically, affecting our measure of the spatial-explicit survival. Finally, while the spatial distribution of cod eggs and larvae during the pelagic phase is mainly determined by environmental factors, the young demersal cod have a certain ability to select their habitat. Thus, density-dependent habitat selection of age-0 cod (e.g., Swain and Wade 1993) may also affect the spatial distribution and the survival at later stages. However, in spite of the challenges encountered in our analysis, the reported impact of top-down and internal control on age-0 cod survival is very robust and corroborated by several independent studies. Thus, we believe that cannibalism and temperature-regulated

22

overlap between adult and young cod, represent an important mechanism through which juvenile cod distribution and survival is regulated in the Barents Sea.

Understanding the spatial pattern of species survival is critical toward their management. In marine ecology there is an increasing awareness toward a more holistic management of marine renewable resources (e.g., Botsford et al. 1997). Such awareness is increasingly reflected in the current emphasis toward the establishment of marine protected areas as a form of resource management (Dayton et al. 2000) – in turn calling for a better understanding of what constitutes habitat quality (Sale et al. 2005). The issue of habitat quality for marine resources has been typically linked with areas of peak potential for individual growth (Brandt et al. 2002), and species abundance (Logerwell et al. 2005) and biodiversity (Roberts et al. 2002, Worm et al. 2003, Fox and Beckley 2005). In our views however, the quality of an habitat is not only defined by the current status of individual, demographic or community metrics, but also by processes that affect the dynamics of these same metrics, such as predator-prey interactions and population survival. The case illustrated for age-0 cod in the Barents Sea is very elucidating: the area typically corresponding to the highest summer-fall density of age-0 cod often coincides with the area of lowest winter age-1 density, which raises the interesting conundrum of what to protect: the present abundance or the potential for a greater survival. Though focused on a single species, the analytical techniques used in this study can be easily applied to other systems and species and should be most useful to understand the joint effects of spatial and temporal environmental variability on species distribution and survival, under incumbent climate and environmental changes.

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24

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Appendix A

Adjustment for diel variability of age-1 cod catches

Young cod are known to vertically migrate on a diel base, which may pose a problem in our analysis of spatial survival. The diel migratory behaviour is particularly pronounced in individuals smaller than 15 cm in length, roughly corresponding to the age-1 stage (Hjellvik et al. 2001), and in deeper waters (Hjellvik et al. 2002). To overcome the potential problem of diel variability we corrected the age-1 bottom trawl catches by a factor (*s(δ)*) related to the sampling bias introduced by migratory behaviour of the age-1 cod. Specifically, let *s* be a smooth function describing the natural logarithm (plus 1) of age-1 cod catches (*x*) in relation to time of the day (*δ*). It is then possible to construct a nonparametric additive regression model (GAM) to reproduce the diel variability of bottom trawl catches:

$$x_{t,(\varphi,\lambda),\delta} = k_t + s(\delta) + \varepsilon_{(\varphi,\lambda)} \tag{1}$$

The quantity k_t defines the average catch of age-1 cod as a function of the year (*t*), and it also accounts for the variability introduced by the yearly changes of age-1 cod abundance (including the one introduced after the 1994 gear change). The term $\varepsilon_{(\varphi,\lambda)}$ is a random error at the latitude φ and longitude λ, assumed to be normally distributed over the sampled grid. The term s(*δ*), defines the anomalies of the cod catches as a function of time of the day. It follows that the quantity:

$$x'_{t,(\varphi,\lambda),\delta} = x_{t,(\varphi,\lambda),1,\delta} - s(\delta) \tag{2}$$

used in the analysis of spatial survival, represents the age-1 cod catches corrected by the bias introduced by the diel variability. The 'mgcv' library of R, version 2.1.1 (Wood 2004) was used to implement the nonparametric regression in (1). The local time (*δ*) was derived from the Greenwich Mean Time (GMT) corrected for local longitude as reported in Hjellvik et al. (2002).

Results of the above analysis indicated that daytime catches of age-1 cod were on average higher than night-time catches (Fig. A1). The found relationship between cod catches and time of the day resembled the one reported in Hjellvik et al. (2001). The procedure applied in this study (Eq. 2) successfully removed the diel trend of age-1 cod catches, as the new established age-1 metric did not contain a diel trend, nor did any of the subsequent models applied on age-0 cod spatial survival.
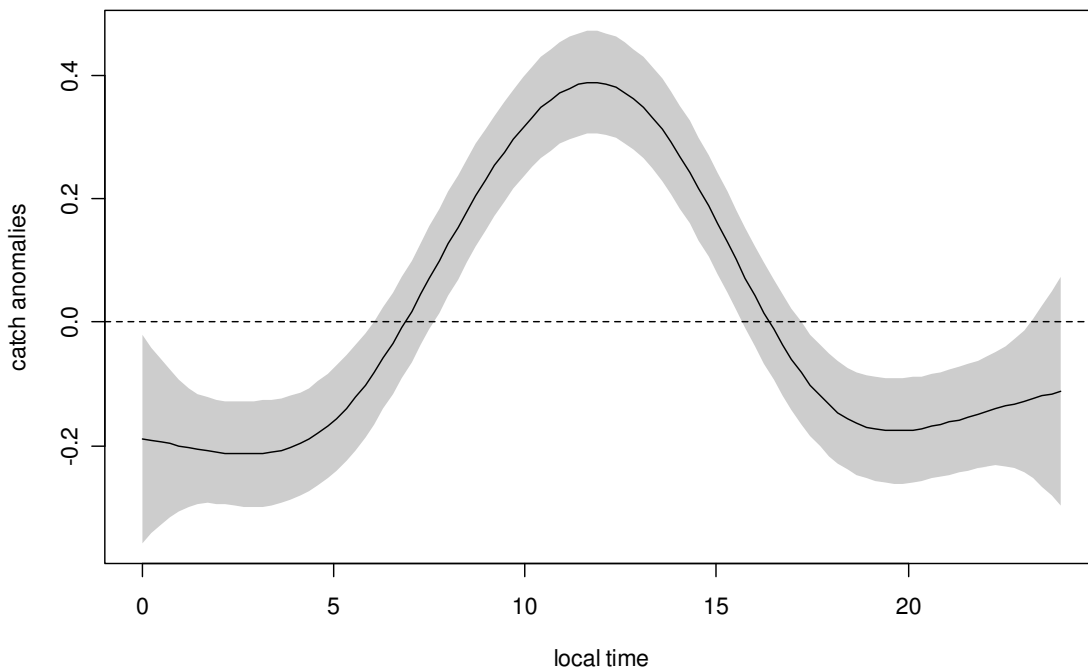
Figure A1 Anomalies in diel variability of log-transformed age-1 cod catches as predicted from a nonparametric model applied to the 1981-2004 surveys. Values above or below the dashed horizontal line respectively have a positive or a negative contribution on average cod catches. The shaded region indicates the 95% point-wise confidence interval. The average log-transformed cod catch was 5.72.

Literature cited

Hjellvik, V., O. R. Godø, and D. Tjøstheim. 2001. Modelling diurnal variation of marine populations. Biometrics 57:189-196.

Hjellvik, V., O. R. Godø, and D. Tjøstheim. 2002. Diurnal variation in bottom trawl catches: does it pay to adjust? Canadian Journal of Aquatic and Fisheries Sciences **59**: 33-48.

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Appendix B

Selection of threshold value

The threshold value for the threshold model formulations (Eq.3 in Methods) was chosen by minimizing the model Generalized Cross Validation – a measure of the mean squared predictive error of the model (Green and Silverman 1994). Namely, we run 20 model formulations within the upper 0.9 and lower 0.1 quintile of the threshold covariate range, and recorded the corresponding GCVs. This procedure ensured that at least 10% of the data are left within one of the two regimes. Finally, we selected the threshold value in correspondence of the lowest GCV. Figure B1 shows the GCV profile for each of the examined threshold formulations.

The so found GCV however, cannot be compared with the GCV of a fully additive formulation, because it does not properly account for the presence of an additional parameter (i.e., the threshold) in the threshold formulation. Thus, to properly compare models with and without threshold we computed the genuine cross validation (CV) as follows. A random sample of 10% of the data was excluded from the observations and the remaining data were used to fit a new threshold model. The so fitted model was then used to estimate the out-of-sample 10% data cases, and the mean squared predictive error was recorded. The same routine was repeated 500 times, with the final CV being the average of all runs.
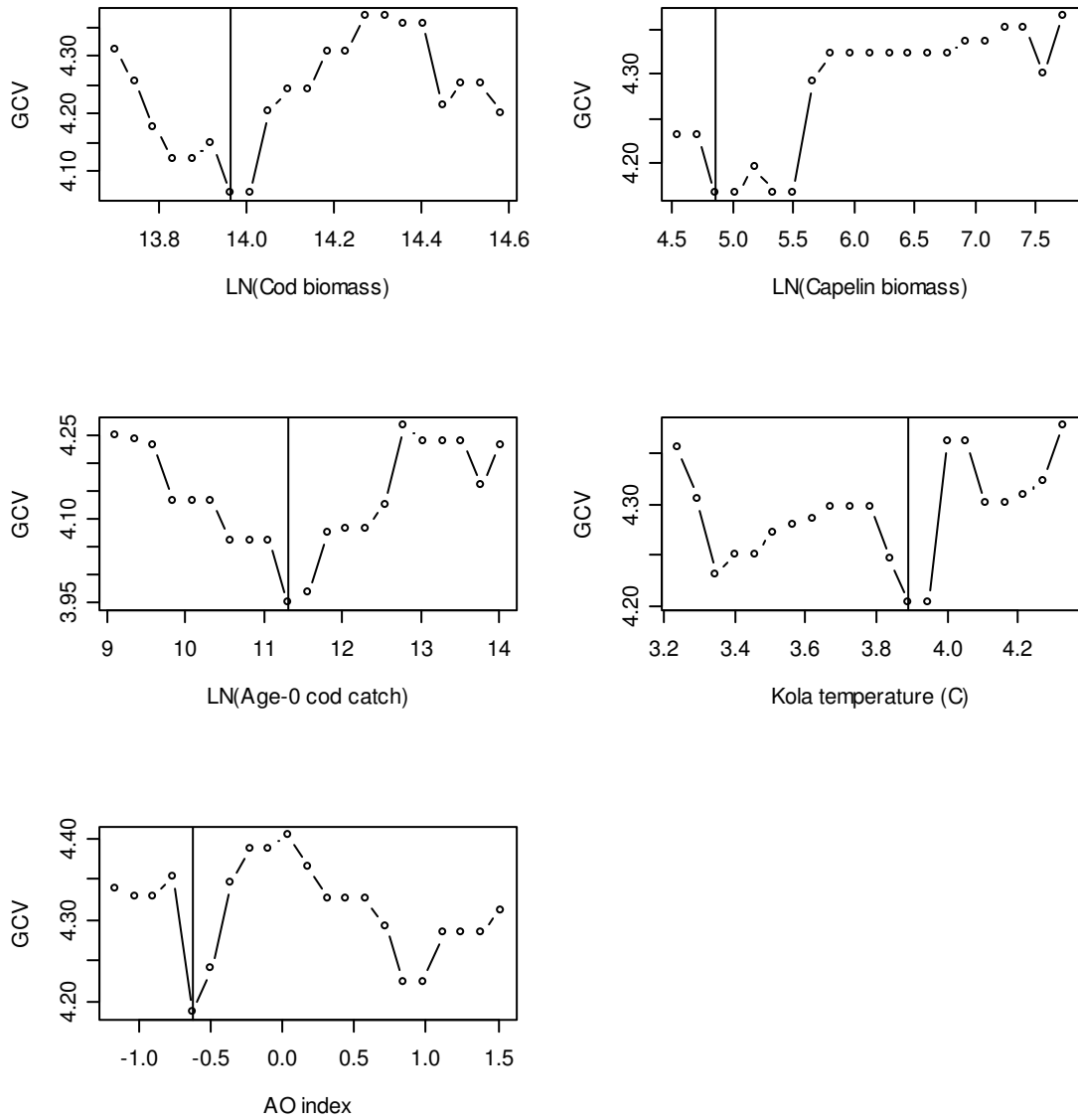
Figure B1 GCV profile for each of the examined threshold formulations. The vertical line indicates the selected threshold value.

Literature cited

Green, P. J., and B. W. Silverman. 1994. Nonparametric regression and generalized linear models: A Roughness Penalty Approach (Chapman and Hall)