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Paper II

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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 aeglefinus*, *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, Gjørseter 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, Gjørseter and Bogstad 1998, Hjermmann 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.

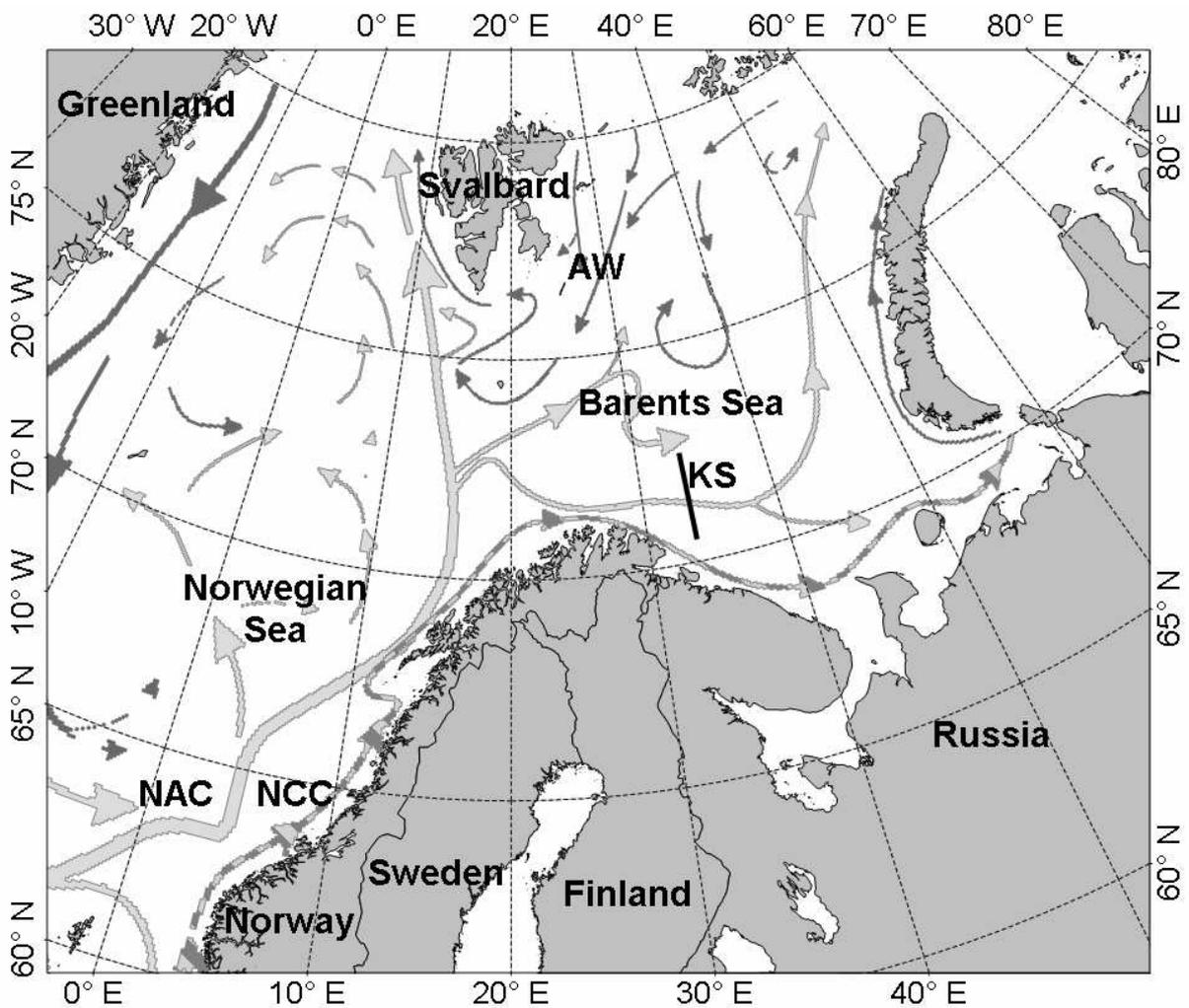


Figure 1 Norwegian Sea and Barents Sea with simplified current system. NAC stands for North Atlantic Current, NCC for Norwegian Coastal Current, AW for Arctic Water, and KS for the Kola section.

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.	Cap^0	Acoustic survey
$C_{t-1,t}^{Mcap}$	Natural logarithm of catch numbers of mature capelin.	Cap^0	Fisheries statistics
Cap_t^0	Natural logarithm of capelin age-0 abundance.	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.	Cod^0	VPA estimate
Cod_t^{SSage}	Mean age in cod spawning stock.	Cod^0	VPA estimate
Cod_t^0	Natural logarithm of cod age-0 abundance.	$Cap^0, Had^0, Her^0, Cod^1, Cap^1, Her^1$	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	Cod^1, Had^1	Bottom trawl survey
Had_t^{SSB}	Natural logarithm of haddock spawning stock biomass.	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.	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.	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.	Her^1	Pelagic trawl survey
L_t^{Her0}	Mean length of herring at age-0.	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.	$Cap^0, Cod^0, Had^0, Her^0, Cap^1, Cod^1, Had^1, Her^1$	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 (°C) 0-200m at the Kola section.	$Cap^0, Cod^0, Had^0, Her^0, Cap^1, Cod^1, Had^1, Her^1$	CTD-data
T^S	Mean summer (June-Aug.) temperature (°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

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:

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

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

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:

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

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

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-validators 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.

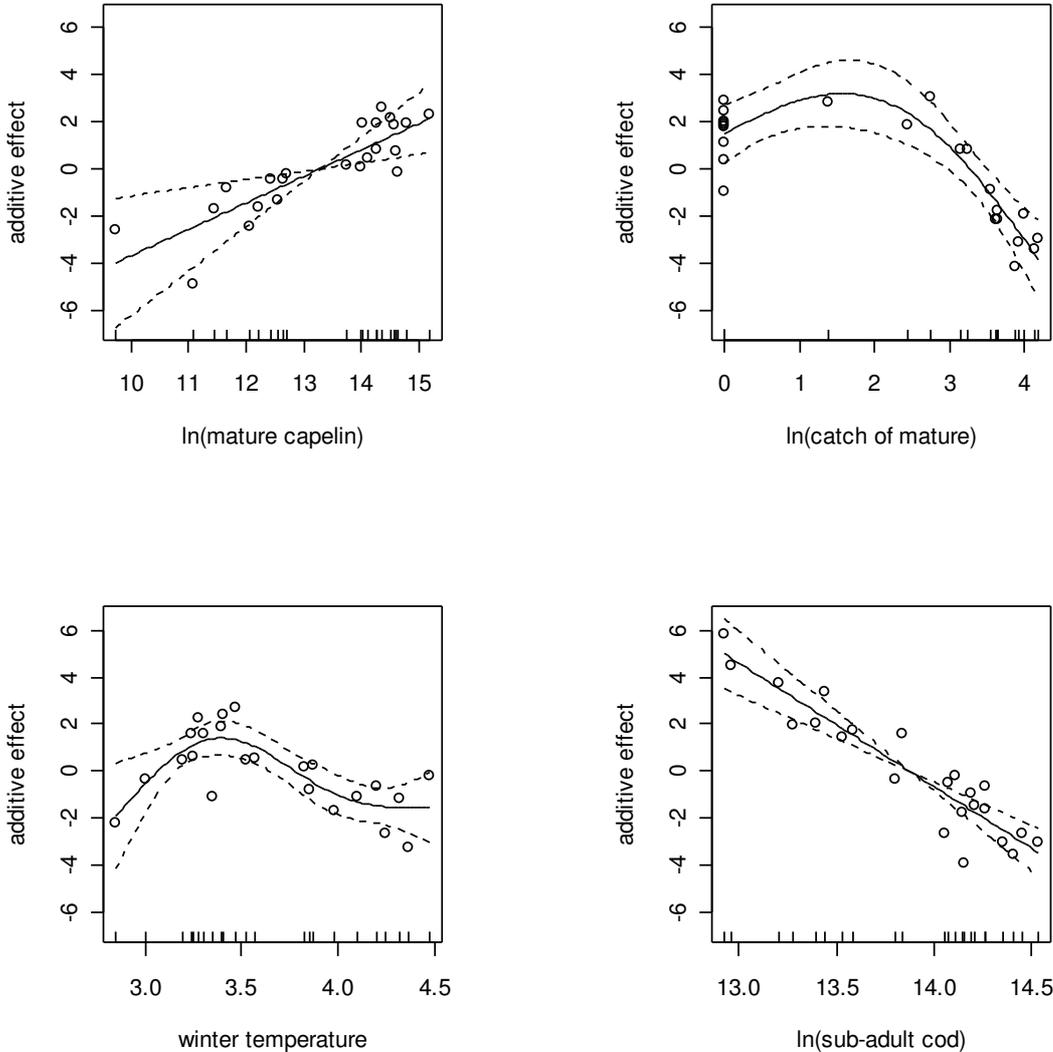


Figure 2 Factors affecting the abundance of capelin at age-0 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

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.

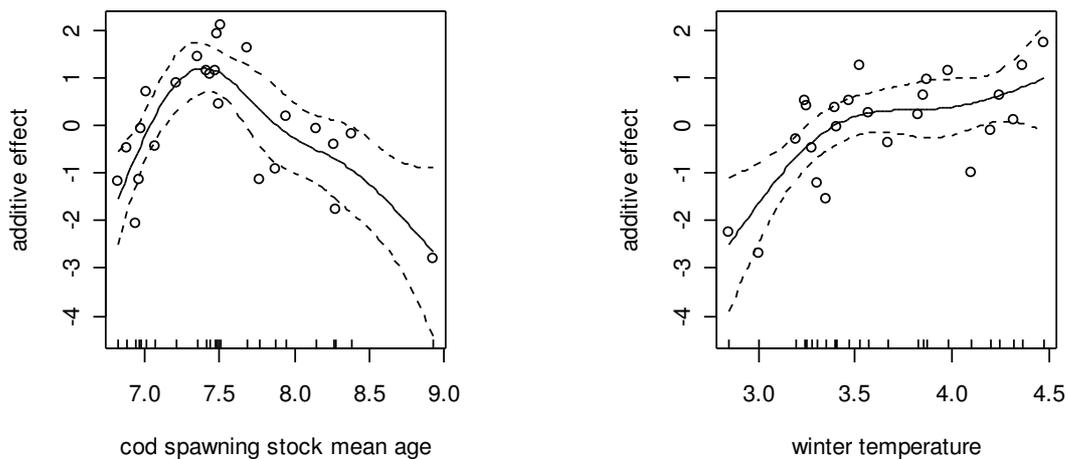


Figure 3 Factors affecting the abundance of cod at age-0 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

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).

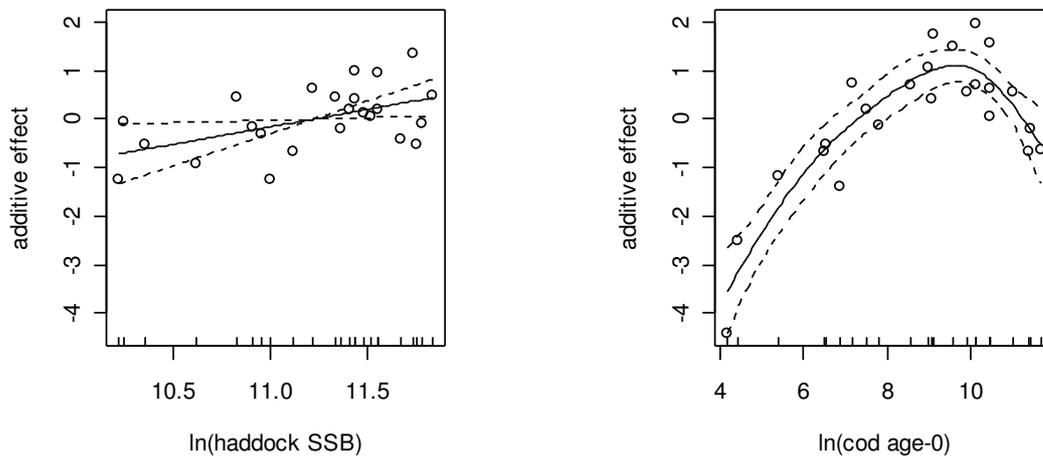


Figure 4 Factors affecting the abundance of haddock at age-0 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

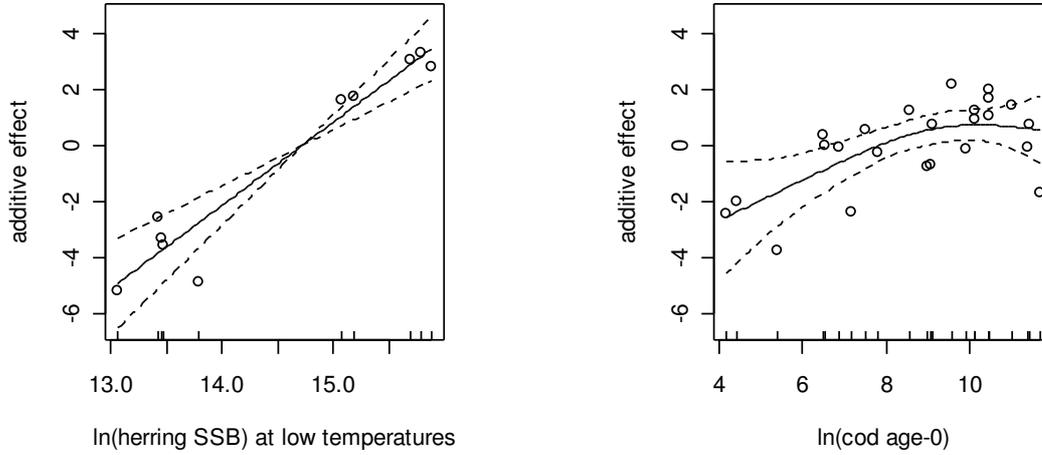


Figure 5 Factors affecting the abundance of herring at age-0 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

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	$Cap_{t+1}^1 = 11.39 + g_1(P_{t+1}^C) + g_2(T_{t+1}^W) + \varepsilon_{t+1} + \begin{cases} , & \text{if } T_{t+1}^W \leq 3.40 \\ f(Cap_t^0), & \text{if } T_{t+1}^W > 3.40 \end{cases}$	0.76	1.07
TGAM	$Cod_{t+1}^1 = \beta_{trawl} + f(Cod_t^0) + \varepsilon_{t+1} + \begin{cases} 2.76, & \text{if } T_{t+1}^W \leq 3.54, \beta_{trawl} = 1.50 \\ 3.66 + g(P_{t+1}^C), & \text{if } T_{t+1}^W > 3.54 \end{cases}$	0.92	0.95
TGAM	$Had_{t+1}^1 = 6.67 + g(T_{t+1}^W) + \varepsilon_{t+1} + \begin{cases} f(Had_t^0), & \text{if } T_{t+1}^W \leq 3.72 \\ , & \text{if } T_{t+1}^W > 3.72 \end{cases}$	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.

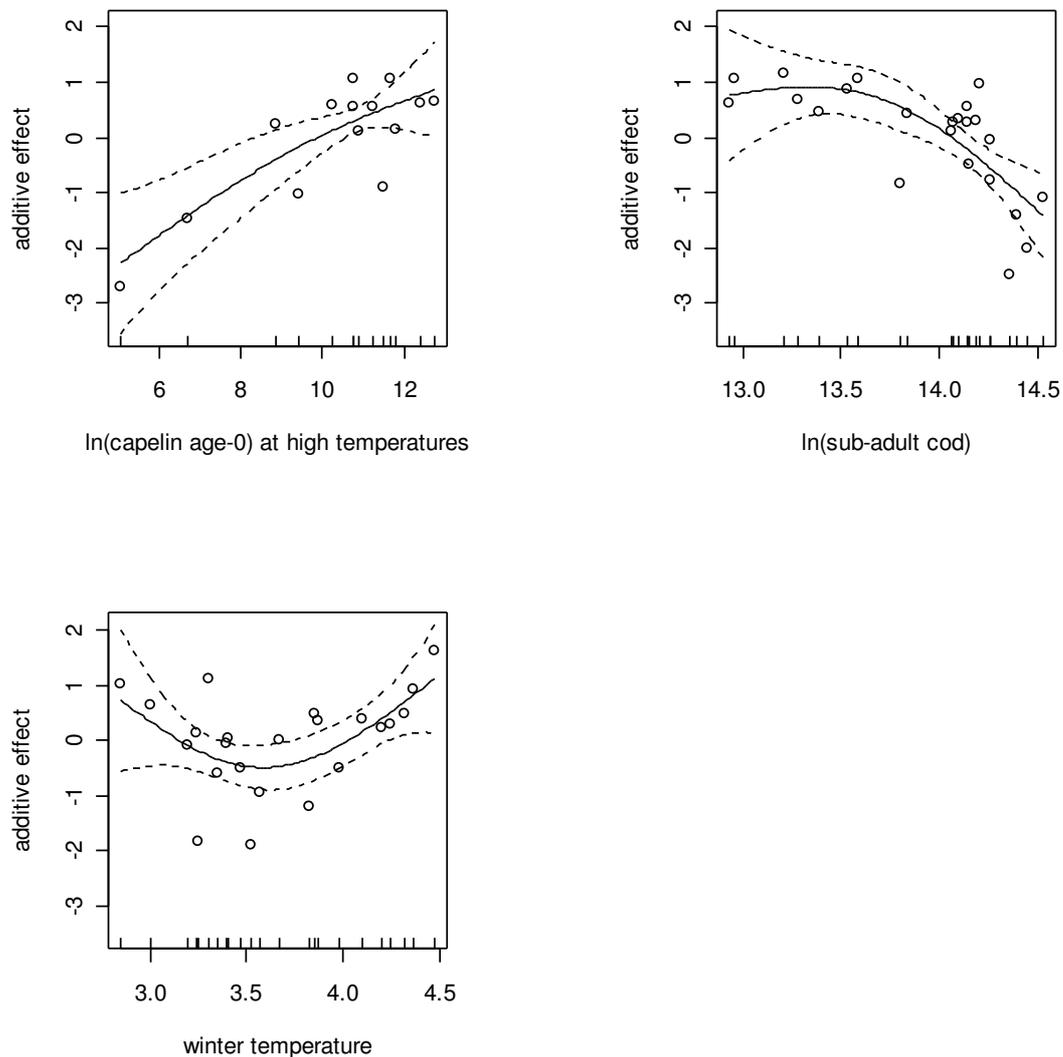


Figure 6 Factors affecting the abundance of capelin at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

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

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.

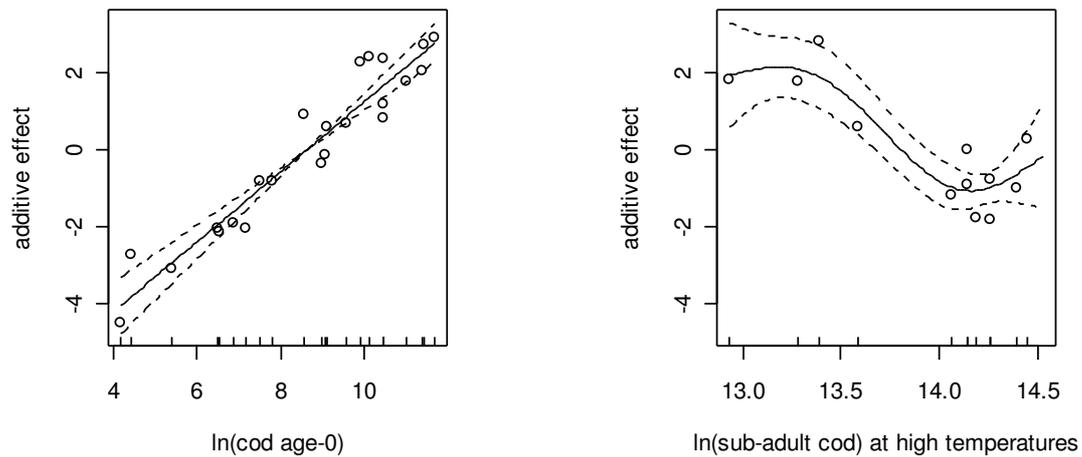


Figure 7 Factors affecting the abundance of cod at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

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.

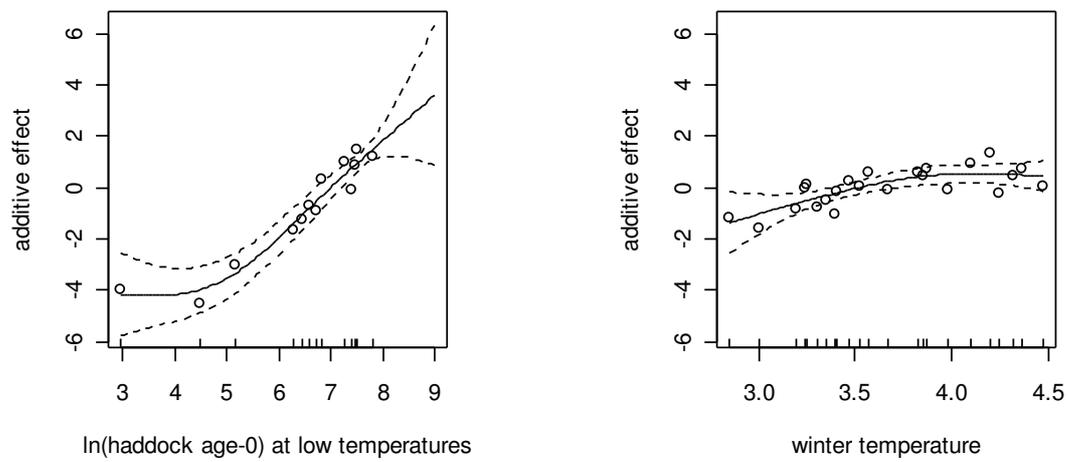


Figure 8 Factors affecting the abundance of haddock at age-1 modeled with TGAM. Dashed lines indicate approximate 95% confidence intervals.

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.

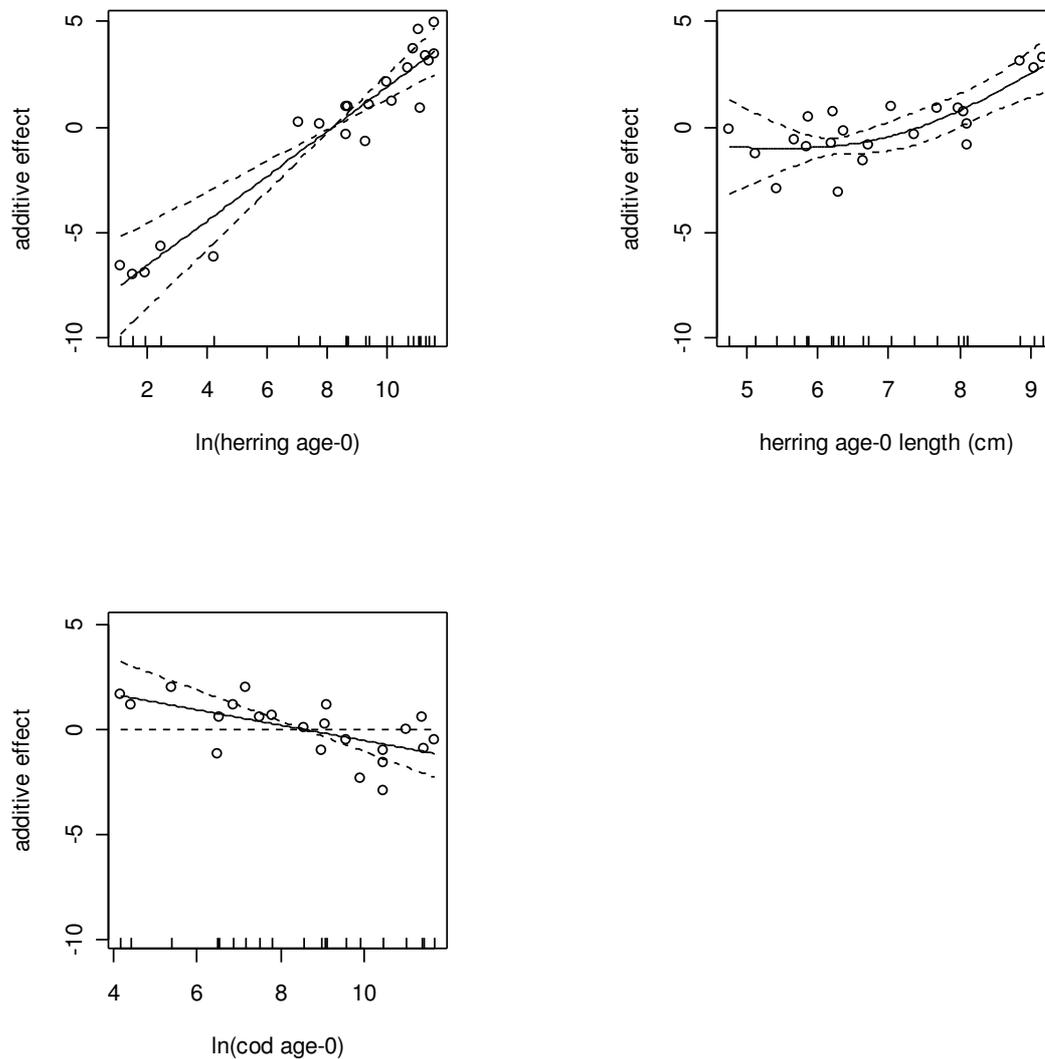


Figure 9 Factors affecting the abundance of herring at age-1 modeled with GAM. Dashed lines indicate approximate 95% confidence intervals.

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 Icelandic 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, Gjørseter 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 (Gjørseter 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

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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