

DENSITY DEPENDENCE AND DENSITY INDEPENDENCE DURING THE EARLY LIFE STAGES OF FOUR 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 nonadditive properties that may have profound dynamic effects. We investigate the importance of population density (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 nonadditive interactions between internal and external variables in the abundance of these two pre-recruitment stages. Our results indicate that, during their first five months of life, cod, haddock, and herring experience higher density-dependent survival 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 influencing 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 subadult 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, rather than as a population phenomenon.

Key words: Barents Sea; *Clupea harengus*; density dependence; density independence; *Gadus morhua*; GAM; *Mallotus villosus*; *Melanogrammus aeglefinus*.

INTRODUCTION

Density dependence is a fundamental concept in the study of fish population dynamics. Density-dependent processes can either be compensatory or depensatory (see Rose et al. 2001). Here, we focus on the impacts of compensatory processes, i.e., those promoting a decrease of population growth at high densities, on recruitment variability in marine fish stocks. The mechanisms causing compensatory effects are generally assumed to be (1) death as a direct effect of competition for limited resources or of an increase in predation at high numbers or (2) death as an indirect effect due to changes in growth rate and condition, in turn causing greater susceptibility to predation, cannibalism, and diseases (Frank and Leggett 1994). 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). Compensatory density dependence is important in management because it acts to stabilize populations and because it implies stock recovery from overexploitation. However, it is still debatable how to properly account for it (Rose et al. 2001). A central challenge is that of determining its actual magnitude (Fogarty et al. 1992, Rose et al. 2001), and variation in response to density-independent factors. For example, density-dependent and density-independent variables may often exhibit interactive (i.e., nonadditive) effects on survival and recruitment (Ciannelli et al. 2004, Stenseth et al. 2004). Such nonlinearities and nonadditive processes may in turn have profound dynamic implications at the population level (May 1976, Ciannelli et al. 2005).

Fish experience biological processes differently, through the different life-history stages. Unfortunately, the most common measure of density dependence in fisheries management is obtained from spawning stock biomass vs. recruitment relationships: two life stages that in most commercial fish species are separated by at least two years and by a variety of contrasting survival

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processes (e.g., reproduction, egg and larval drift, larval feeding and growth, juvenile predation and settlement, and so on). Integrating over so many life stages may veil the real contribution of density-dependent and density-independent mechanisms to species survival. Rothschild (2000) suggested using life-history theory as a framework for understanding and predicting the magnitude of compensation in populations. For example, density-dependent mortality caused by predation is most likely to be important early in the life-history, while density-dependent growth caused by bottom-up processes in the adult stages may influence the reproduction of populations (Lorenzen and Enberg 2002, Munch et al. 2005).

We investigate the importance of initial population density and environmental conditions for the abundance of age-0 (four to five months old) and age-1 stages of four fish species in the Barents Sea via a comparative approach. 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 (TGAM; Ciannelli et al. 2004). The latter is a modeling 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 nonadditive 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, nonadditive or nonlinear.

METHODS

Study species

Capelin (*Mallotus villosus*), northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring spawning herring (*Clupea harengus*) are all commercially important fish species in Norwegian waters, spawning along the Norwegian shelf and slope regions and using the Barents Sea as their nursery area (Fig. 1). Capelin and herring are demersal spawners while cod and haddock spawn pelagic eggs. Larvae of all four species are transported northward along the coast of Norway, and then eastward into the Barents Sea, by the Norwegian Coastal Current or the North Atlantic Current (Fig. 1). Calanoid copepods represent important prey to larvae and early juveniles of all species in the study (Helle 1994, Huse and Toresen 1996, Gaard and Reinert 2002). Thus, it is possible that density dependence through inter- and intra-specific competition for food is present and underscores the importance of viewing the problem of species recruitment variability as a community, rather than as a population phenomenon.

The data

The variables used in the analysis of early life stage abundances are listed in the Appendix and time series of

the different life stages are shown in Fig. 2. An international 0-group (age-0) 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 the early 1980s. 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 (Institute of Marine Research/Polar Research Institute of Marine Fisheries and Oceanography 2005: Table 2.3). All estimates concerning age-0 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.

Capelin are measured acoustically in September–October, and spawn the following spring. In addition to age specific abundance indices, we also applied the estimated biomasses of maturing individuals. Individuals were assumed to be maturing when they were longer than 14 cm. The capelin catches used are the natural logarithm of commercial catches of maturing individuals in the period from October to the time of spawning. Both the abundance estimates and stock biomasses were log-transformed in the analysis.

Since 1981, a combined acoustic and bottom trawl survey has been carried out in January–March (4–6 weeks) to obtain winter age specific abundance estimates of cod and haddock. 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 were retrieved from the bottom trawl indices (International Council for the Exploration of the Sea 2004a). The spawning stock biomasses (SSB) of cod and haddock and the numbers of cod age 3–6 are from the Virtual Population Analysis (VPA; Quinn and Deriso 1999:323) estimates by the Arctic Fisheries Working Group (International Council for the Exploration of the Sea 2004a).

Juvenile herring are measured acoustically in May–June when distributed in the southern part of the Barents Sea. There were no measurements of the 1980–1981 and 1986–1987 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 age-0 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 International Council for the Exploration of the Sea (2004b) and supplemented with information from Toresen et al. (1998). Herring SSB estimates are from the SeaStar assessment by the Northern Pelagic and Blue Whiting Fisheries Working

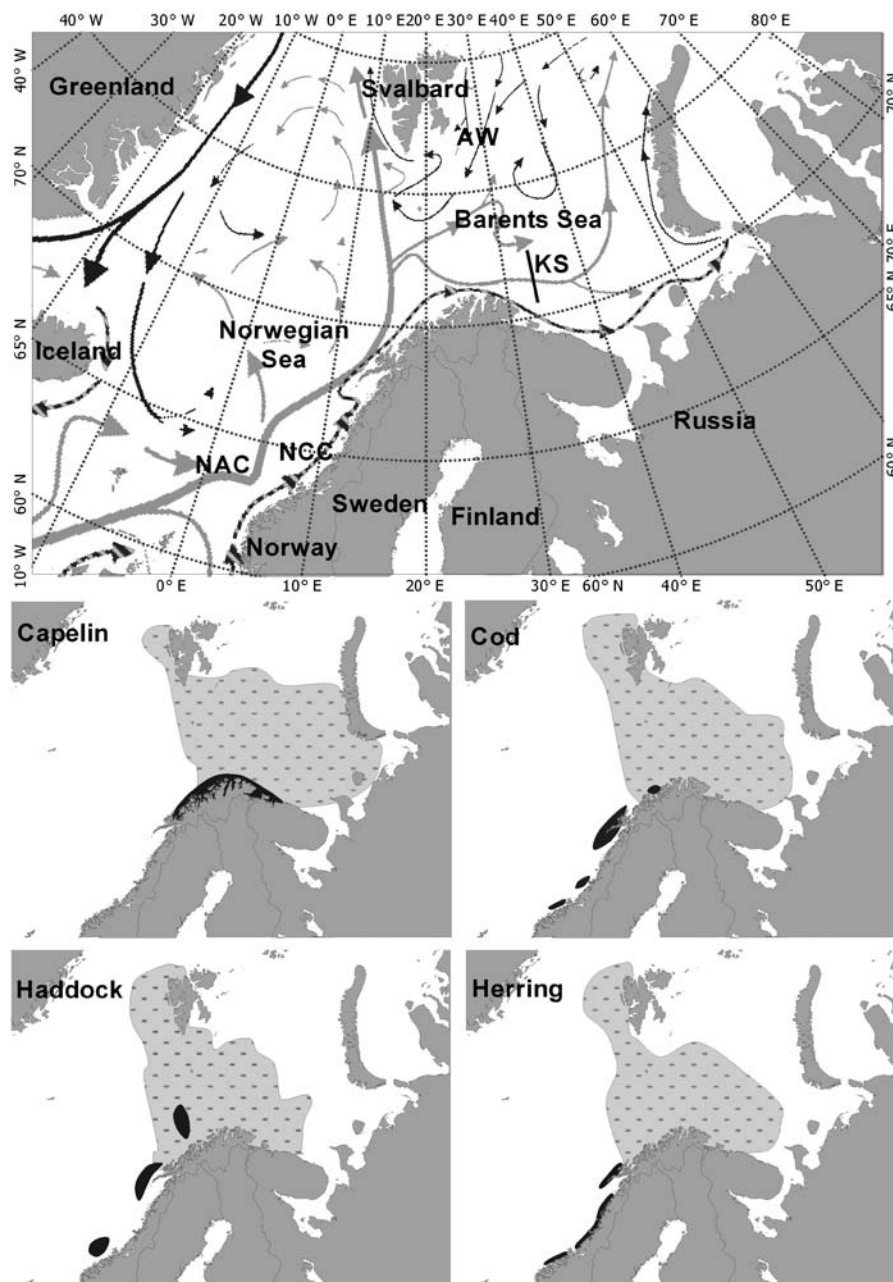


FIG. 1. The upper panel shows the Norwegian and Barents seas with simplified current systems: NAC, North Atlantic Current; NCC, Norwegian Coastal Current; AW, Arctic Water; KS, Kola section. Lower panels show the main spawning grounds (dark-shaded areas) and average distribution of age-0 (light-shaded areas) capelin, cod, haddock, and herring.

Group (International Council for the Exploration of the Sea 2004b). The weighted mean age in the spawning stock of herring as well as cod and haddock were estimated using biomasses at age as weights.

The temperature series refer to 0–200 m average sea water temperature along the Kola section (70°30' N to 72°30' N along 33°30' E) during winter (December–March) and summer (June–August) (Tereshchenko 1996; Polar Research Institute of Marine Fisheries and

Oceanography, *personal communication*). The Kola temperature time series has been shown to reflect the relative large-scale interannual variations in the Barents Sea very well (Dippner and Ottersen 2001).

The models

We investigated the underlying processes determining the year-class strength at the age-0 and age-1 stage of capelin, cod, haddock, and herring. These processes

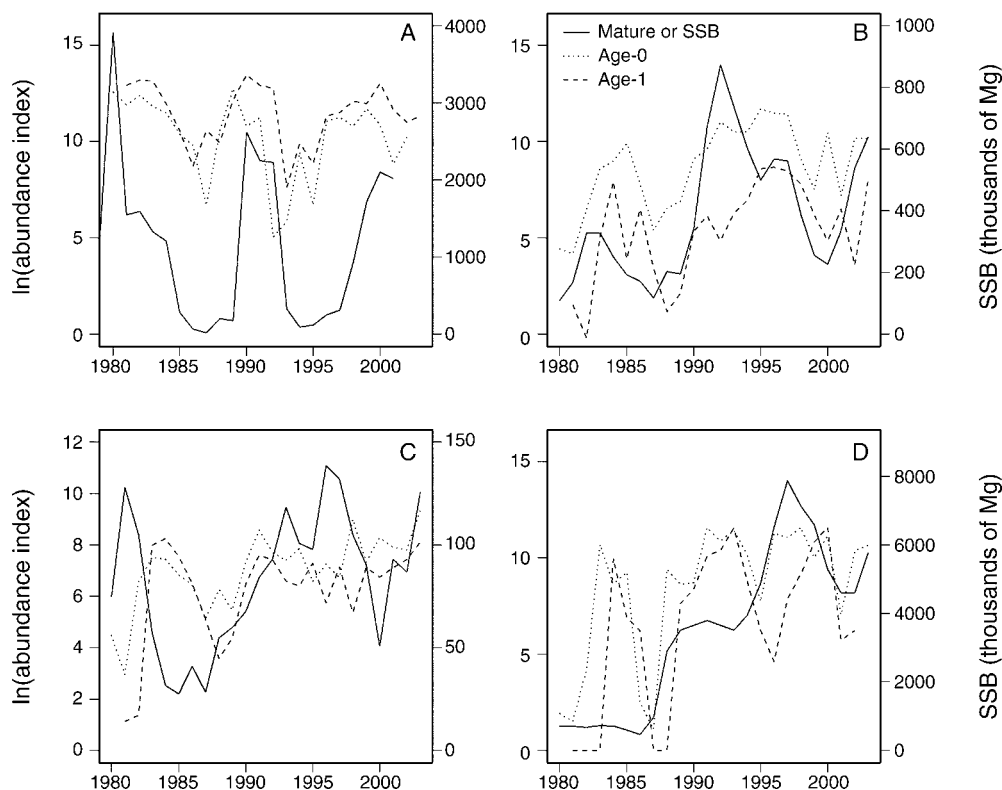


FIG. 2. Time series of age-0 and age-1 abundance indices, and spawning stock biomasses (SSB) for (A) capelin, (B) cod, (C) haddock, and (D) herring used in the models.

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 nonadditive 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 $a + 1$. Then the generalized additive formulations, for the age-0 and age-1 abundance become, respectively,

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

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

The coefficient α^a defines the average abundance at stage a and the term ε is random error assumed to be normally distributed. Note that each smooth function is assumed to be centered, i.e., of zero mean over the data, for model identifiability. Eq. 1 is a nonparametric variation

of the traditional parametric approach for analyzing stock-recruitment data, for example the generalized Ricker formulation (Quinn and Deriso 1999: 91). Generalized additive models have the benefit of increased modeling flexibility and have been increasingly employed in fisheries research (Ciannelli et al. 2004, Venables and Dichmont 2004, Ciannelli and Bailey 2005). Note that we use the convention that functions with the same symbol but different arguments are distinct. For example, $f(X_t^{\text{SSB}})$ and $f(X_t^0)$ are different functions. It is important to note that in our statistical models a nonsignificant relationship between SSB and age-0 abundance (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 and shape).

In deciding which smoothing terms should be retained in the final models, we applied a backward selection strategy. Specifically, we started with a model including all the covariates considered relevant to a specific modeled stage, and removed them 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 prediction error) was minimized (Wood and Augustin 2002). The relevance of the covariates used in the initial model formulations was based on a-priori knowledge. In general, for each

TABLE 1. Final formulations, adjusted R^2 (i.e., proportion of variance explained), and genuine cross validation of the best models for age-0 abundances per species.

Model	Formulations	R^2 †	Genuine cross validation†
GAM	$\text{Cap}_t^0 = 10.175 + f_1(\text{Cap}_{t-1}^{\text{Mat}}) + f_2(\text{Cap}_{t-1}^{\text{Mcap}}) + g_1(T_t^{\text{W}}) + g_2(P_t^{\text{C}}) + \varepsilon_t$	0.72 (0.73)	3.34 (3.88)
TGAM	$\text{Cod}_t^0 = f(\text{Cod}_t^{\text{SSB}}) + g(T_t^{\text{W}}) + \varepsilon_t + \begin{cases} 7.58 & \text{if } \text{Cod}_t^{\text{SSB}} \leq 12.78 \\ 10.28 & \text{if } \text{Cod}_t^{\text{SSB}} > 12.78 \end{cases}$	0.84 (0.84)	1.45 (1.52)
GAM	$\text{Had}_t^0 = 7.01 + f(\text{Had}_t^{\text{SSB}}) + g(\text{Cod}_t^0) + \varepsilon_t$	0.80 (0.86)	0.66 (0.68)
TGAM	$\text{Her}_t^0 = g(\text{Cod}_t^0) + \varepsilon_t + \begin{cases} 7.64 + f(\text{Her}_t^{\text{SSB}}) & \text{if } T_t^{\text{W}} \leq 3.44 \\ 9.41 & \text{if } T_t^{\text{W}} > 3.44 \end{cases}$	0.88 (0.78)	2.25 (3.73)

Note: Abbreviations and variables are: Cap, capelin; Cod, cod; Had, haddock; Her, herring; C^{Mcap} , catch of mature capelin; T^{W} , winter temperature; P^{C} , predator (cod age 3–6); ε , error term. Superscripts are: 0, age-0; Mat, maturing fish; SSB, spawning stock biomass; SSage, mean age in spawning stock; t , year.

modeled stage we tried to capture the following ecological processes: density dependence (SSB or age-0), abiotic forcing (Kola temperature), predation, and competition. In addition, a few models contained a covariate expressing the age diversity of the parental stock, mean length at age-0 and the positioning of the age-0 stage (Appendix).

The threshold nonadditive 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 occur in the functions (from f_1 to f_2 , $g_{1,j}$ to $g_{2,j}$), in the intercept (from α_1 to α_2), or in a combination of both. Then the TGAM formulations become:

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

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

The threshold level (r) of the covariate e is chosen by minimizing the GCV score over an interval defined by the 20 to 80 percentiles of the covariate e . The procedure applied for the search of the threshold value is illustrated in Ciannelli et al. (2004). We were interested in capturing changes of biotic processes of population control as a function of abiotic variables. Consequently, temperature thresholds were applied on density-dependent functions, for example on $f(X_t^{\text{SSB}})$, or on a selection of biotic variables, such as predation and competition, that were likely to be affected by temperature.

The best model approach, GAM or TGAM, was determined in each case according to the (genuine) cross-validatory squared prediction error (see Ciannelli et al. [2004] for details).

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 Tables 1 and 2, respectively. For the age-0 abundance models there is no general trend indicating which model approach (GAM or TGAM) 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 of the best models for age-1 abundances per species.

Model	Formulations	R^2 †	Genuine cross validation†
TGAM	$\text{Cap}_{t+1}^1 = 11.39 + g_1(P_{t+1}^{\text{C}}) + g_2(T_{t+1}^{\text{W}}) + \varepsilon_{t+1} + \begin{cases} 0, & \text{if } T_{t+1}^{\text{W}} \leq 3.40 \\ f(\text{Cap}_t^0), & \text{if } T_{t+1}^{\text{W}} > 3.40 \end{cases}$	0.76 (0.77)	1.07 (1.16)
TGAM	$\text{Cod}_{t+1}^1 = \beta_{\text{trawl}} + f(\text{Cod}_t^0) + \varepsilon_{t+1} + \begin{cases} 2.76, & \text{if } T_{t+1}^{\text{W}} \leq 3.54, \beta_{\text{trawl}} = 1.50 \\ 3.66 + g(P_{t+1}^{\text{C}}), & \text{if } T_{t+1}^{\text{W}} > 3.54 \end{cases}$	0.92 (0.91)	0.95 (1.68)
TGAM	$\text{Had}_{t+1}^1 = 6.67 + g(T_{t+1}^{\text{W}}) + \varepsilon_{t+1} + \begin{cases} f(\text{Had}_t^0), & \text{if } T_{t+1}^{\text{W}} \leq 3.72 \\ 0, & \text{if } T_{t+1}^{\text{W}} > 3.72 \end{cases}$	0.93 (0.89)	0.96 (1.13)
GAM	$\text{Her}_{t+1}^1 = 6.46 + f_1(\text{Her}_t^0) + f_2(L_t^{\text{Her}0}) + g(\text{Cod}_t^0) + \varepsilon_{t+1}$	0.92 (0.93)	1.75 (2.29)

Notes: β_{trawl} is due to a change in survey gear in 1994. Variables are as defined in Table 1.

† Values for the next best models are in parentheses.

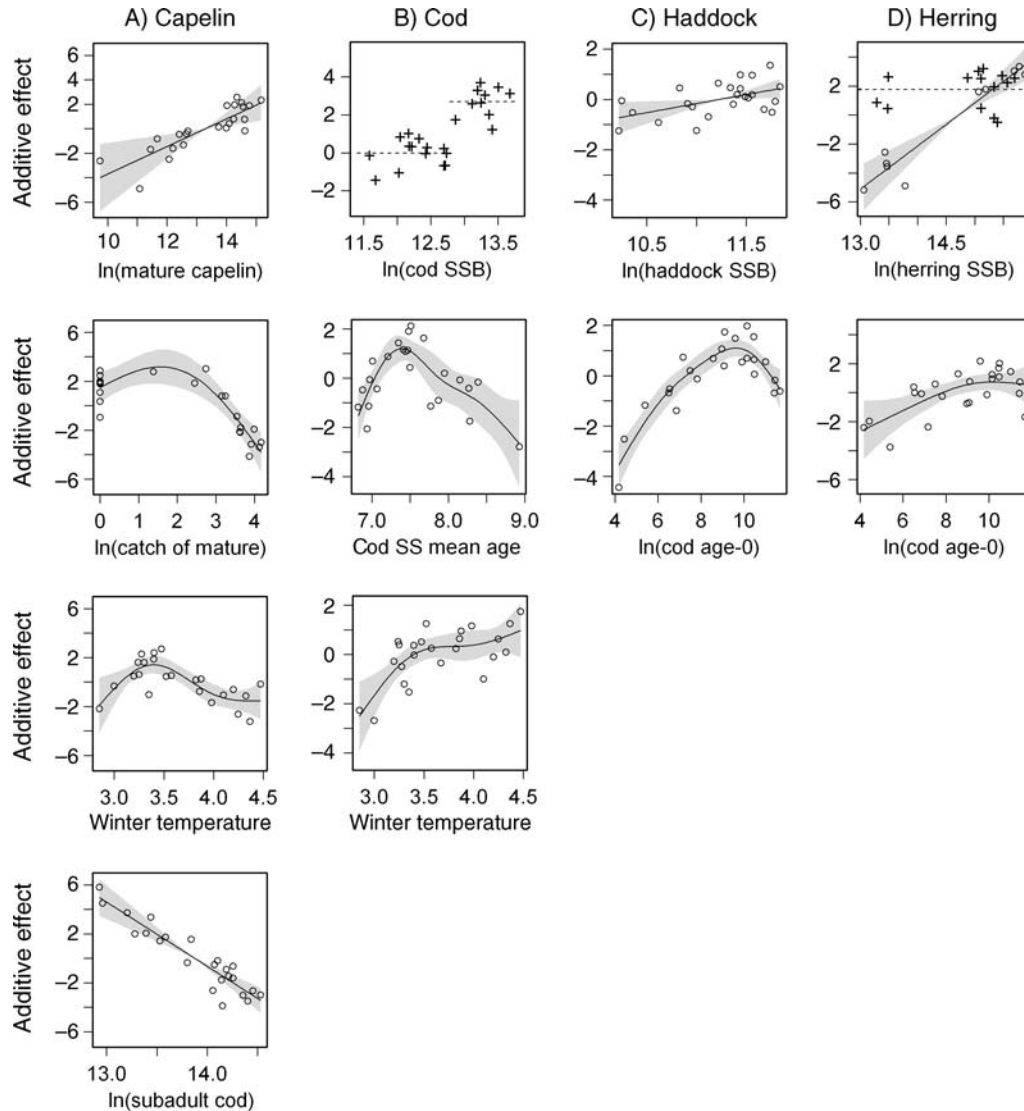


FIG. 3. Results of generalized additive modeling (GAM) and threshold (TGAM) modeling of effects on age-0 abundance. Values on the y-axis indicate the effect of the x-axis covariate on the age-0 abundance anomalies (i.e., age-0 abundance minus mean). Model predicted values are given by the sum, at corresponding locations, of all covariate effects with the average abundance (see Eqs. 1 and 3 in *Methods*). The shaded areas indicate the pointwise 95% CI. All significant functional effects are shown as a continuous line. Dashed lines, when applicable, indicate the difference in average population densities between the two regimes defined by the TGAM formulation. Open circles and crosses are the partial residuals around the significant and nonsignificant covariate effects, respectively. (A) For capelin, effects of mature capelin, commercial catches of mature capelin, winter Kola temperature, and subadult cod. (B) For cod, effects of spawning stock biomass (SSB), mean age in the cod spawning stock, and winter Kola temperature. Note that, in this case, SSB only affected the average age-0 abundance (see Table 1). (C) For haddock, effects of haddock SSB and age-0 cod abundance, as predicted from the GAM. (D) For herring, effects of herring SSB during low (circles and solid line) and high (plus signs and dotted line) temperatures, and age-0 cod abundance.

Age-0 abundance

The age-0 capelin model was unique because there was 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 1 October 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 cross validation value. As expected, both catches of the maturing stock and predation by cod had negative effects, while the biomass of the maturing stock had a positive effect (Fig. 3A). 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.

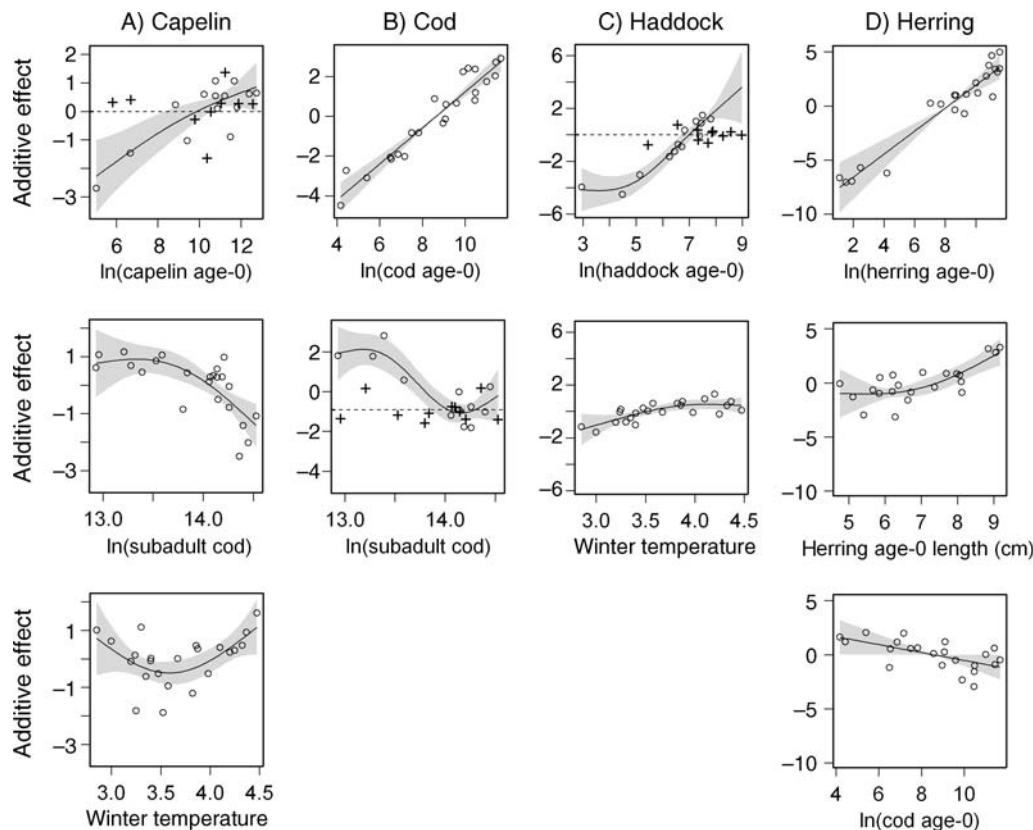


FIG. 4. Results of GAM and TGAM modeling of effects on age-1 abundance. (A) For capelin, effects of age-0 capelin abundance during low (plus signs and dotted line) and high (circles and solid line) temperatures, subadult cod abundance, and winter Kola temperature. (B) For cod, effects of age-0 cod abundance and subadult cod abundance during low (plus signs and dotted line) and high (circles and solid line) temperatures. (C) For haddock, effects of age-0 haddock abundance during low (plus signs and dotted line) and high (circles and solid line) temperatures and winter Kola temperature. (D) For herring, effects of age-0 herring abundance, herring age-0 mean length, and age-0 cod abundance. See the legend of Fig. 3.

Age-0 cod abundance was marginally better modeled by the TGAM formulation, with spawning stock biomass as a discrete effect (Table 1), than the alternative GAM formulation where spawning stock biomass had a positive effect. The mean age of the spawning stock had a dome shaped effect with an optimum around 7.5 years (Fig. 3B). 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.

Age-0 haddock and herring showed a similar response to temperature as age-0 cod. However, when temperature was substituted by age-0 cod abundance, the haddock and herring models gave better fit to the data and lower genuine cross validation values. These results suggested that there are other underlying factors in addition to temperature that affect age-0 abundance of haddock and herring.

Age-1 abundance

Capelin age-0 abundance had a positive effect on the abundance at age-1, but only at temperatures higher than 3.4°C (Fig. 4A), at lower temperatures age-0 abundance was nonsignificant in the model. The temperature effect was U shaped with a minimum also at about 3.4°C. High abundance of subadult cod (age 3–6) had a negative effect on the survival of age-0 capelin.

The trawl gear used to survey age-1 cod and haddock changed in 1994. This change was included in the analysis as a categorical variable (1 and 2) distinguishing between the two trawl gears. For cod, the gear change resulted in an increase of age-1 abundance, indicating greater catch efficiency of the post-1994 gear, while for haddock the gear change showed no significant effects. Abundance of age-0 cod had a strong positive and linear effect on age-1 cod abundance (Fig. 4B), 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 nonadditive model showed that cannibalism had a negative and nonlinear effect only during high

temperature regimes, indicating an indirect negative effect during warm regimes.

Age-0 abundance had a positive effect on age-1 haddock abundance only at low temperatures, indicating density-dependent survival from age-0 at high temperatures. In turn, low temperatures had a negative effect on survival of haddock (Fig. 4C), while we found no effect of predation by subadult cod.

Herring was the only species where length at age-0 had a positive effect. Longer fish resulted in better survival to age-1 (Fig. 4D). 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 suggests that there is competition between cod and herring.

DISCUSSION

Our analysis indicates that spawning stock biomass, temperature, and predation are important factors in determining year-class strength at the early life stages. In the following, we discuss the effects in the order given above. We found indications of strong density dependence in the determination of year-class strength at age-0 for cod, haddock, and herring and at age-1 for capelin and haddock. It is difficult to draw conclusions regarding which density-dependent mechanisms are at play (i.e., direct or indirect) based on the limited time series available to us.

Increased competition for food and increased predation at high densities, also from species not included in the models, are factors that will contribute to density dependence. For example, the frequency of occurrence of cod cannibalism in the Barents Sea increases with the abundance of juvenile cod (Bogstad et al. 1994) and a spatial analysis shows that survival of age-0 cod is negatively affected by their own density (Ciannelli et al. 2007). Our results indicate that age-0 cod have a negative effect on age-0 haddock and herring at high densities. This may be caused by increased competition for food. Higher temperature is an indicator of increased production and advection of zooplankton in the Barents Sea, in turn resulting in 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, 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. Our results also 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. Age-1 haddock show density-dependent survival at high temperatures, which may be caused by increased competition from strong year-classes of cod and herring.

With the exception of capelin, we found a positive effect of water temperature on the abundance of the age-0 stage. A relationship between temperature and recruitment has been shown by numerous studies and for several species (Sundby 2000, Ottersen and Stenseth 2001, MacKenzie and Köster 2004). 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 possible that temperature acts as a proxy for available food for early life stages. However, it is also possible that temperature has a positive effect directly 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. We found a negative effect of temperature on age-0 capelin. This is in agreement with earlier findings suggesting that in cold years capelin uses the easterly spawning grounds, which is beneficial for avoiding predators (Hamre 1994).

High densities of potential predators (i.e., subadult cod) have a negative effect on the abundances of age-1 capelin and cod. Our analysis indicates that cod cannibalism on stages between age-0 and age-1 has a greater effect during warm years. This may be caused by a greater overlap between subadult cod and age-1 cod under such conditions. It is shown that cod have a more eastward distribution in warm years (Ottersen et al. 1998) and a spatial analysis shows that age-0 cod survival is lowest in areas where the abundance of larger cod is highest (Ciannelli et al. 2007). Behavioral traits of age-0 stages may also mediate the predation effect. For example, cod and haddock start migrating towards the bottom gradually throughout the autumn (Bergstad et al. 1987) and temperature may influence the timing of settlement indirectly through growth or increased abundance of food. If food is abundant in the water column they may choose to delay the migration towards the bottom where the predators are located (Bailey 1989).

The mean age in the cod spawning stock showed a dome shaped effect on the age-0 abundance. Compared to first-time spawners, older northeast Arctic cod arrive earlier on the spawning grounds, spawn over a longer time span, produce disproportionately more eggs with a wider range of vertical distribution and lower mortality (Solemdal 1997, Ottersen et al. 2006 and references therein). It is thus believed that a spawning stock with a higher mean age will produce more offspring. However, 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 combination of the increased fertility of older fish and the skewed sex ratio at higher (domination of females) extremes. These results have implications for management, highlighting the importance of maintaining a diverse age structure in the spawning stock.

Some discussion on the data limitations is appropriate. The winter bottom trawl survey is often, and especially in cold years, restricted by the ice border in the north and east. 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 increase of average age-1 cod abundance found during warm years. 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). Age-1 haddock are distributed further southwest than age-1 cod and thus are less influenced by the ice border. Small cod and haddock also show strong diurnal variation in catchability in the winter bottom trawl survey because of vertical migration (Hjellvik et al. 2004). The problems with varying ice coverage and diurnal migration demonstrates that the winter bottom trawl survey is not optimal for surveying age-1 cod and haddock abundance and thus caution is needed when drawing conclusions based on these data.

We have shown how the intensity of density dependence can change over temporally distinct environmental regimes and through different life-history stages. In management of marine fish stocks it is important to have a mechanistic understanding of the interactions between environmental and demographic 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, as we have shown here, 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 scenarios for high and low temperature regimes.

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APPENDIX

Table of covariates used in the modeling (*Ecological Archives* E088-042-A1).