Paper III

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Lorenzo Ciannelli, Gjert E. Dingsør, Bjarte Bogstad, Geir Ottersen, Kung-Sik Chan, Harald Gjøsæter, and Nils Chr. Stenseth, Ecology (ISSN 0012-9658)

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.

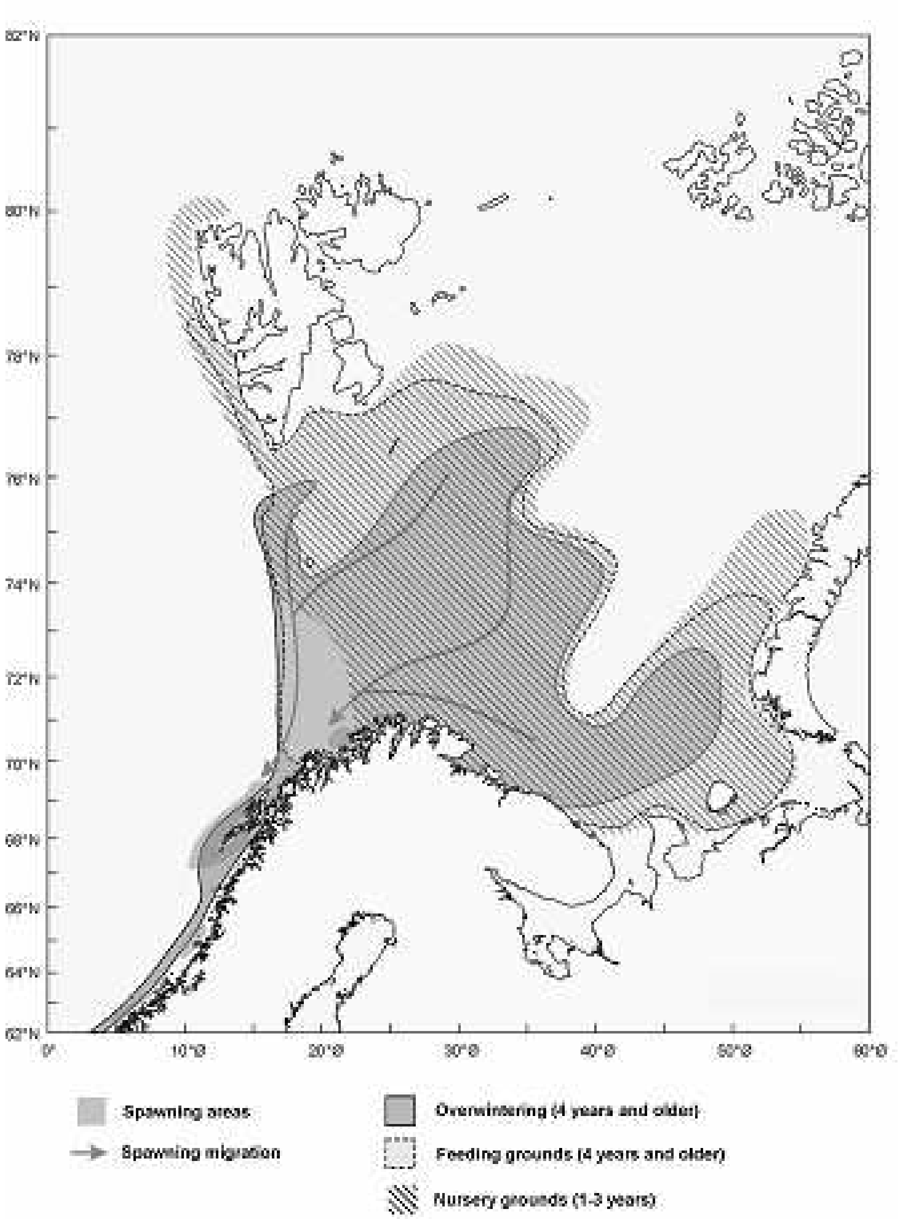

Figure 1 Spawning, overwintering, feeding and nursery areas for Northeast-arctic cod. The arrows indicate spawning migration patterns.

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 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^{o}N and 15.0-51.0^{o}E, with increments of 0.8^{o} and 1.8^{o} 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:

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

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:

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

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,

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

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).

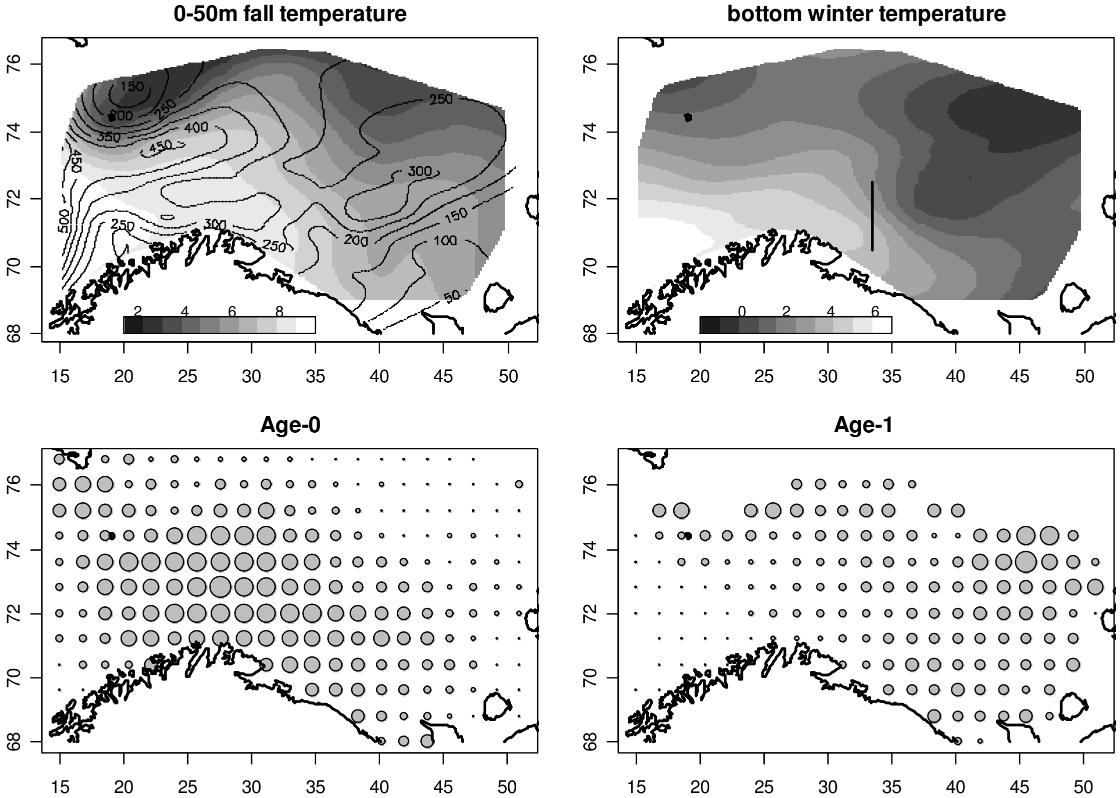

Figure 2 Average distribution of 0-50 m average fall water temperature (top left), winter bottom temperature (top right), age-0 (bottom left) and age-1 (bottom right) cod standardized catches. The area of the circles, in the lower two panels is proportional to the log-transformed and effort-standardized 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.

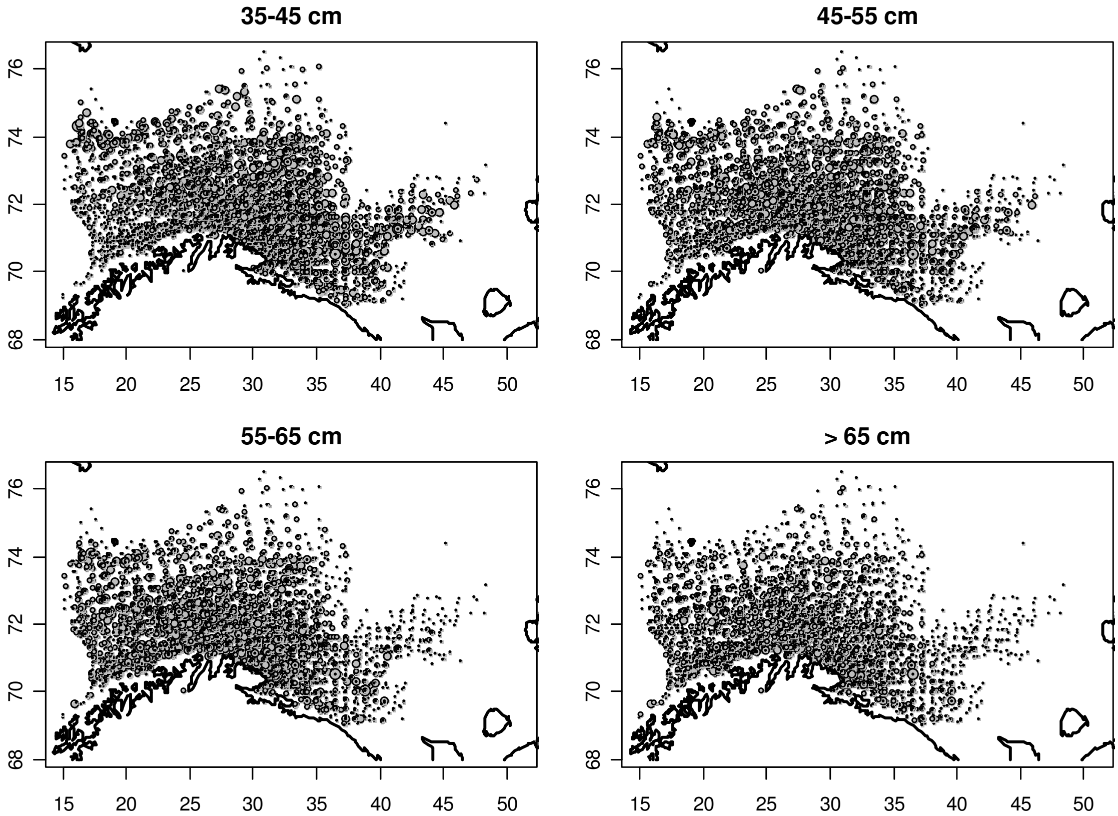

Figure 3 Average distribution of adult cod (1981-2005), during the winter survey, partitioned by size categories. The area of the circles is proportional to the log-transformed and effort-standardized catches.

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^o longitude to the east and by 74^o 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).

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.

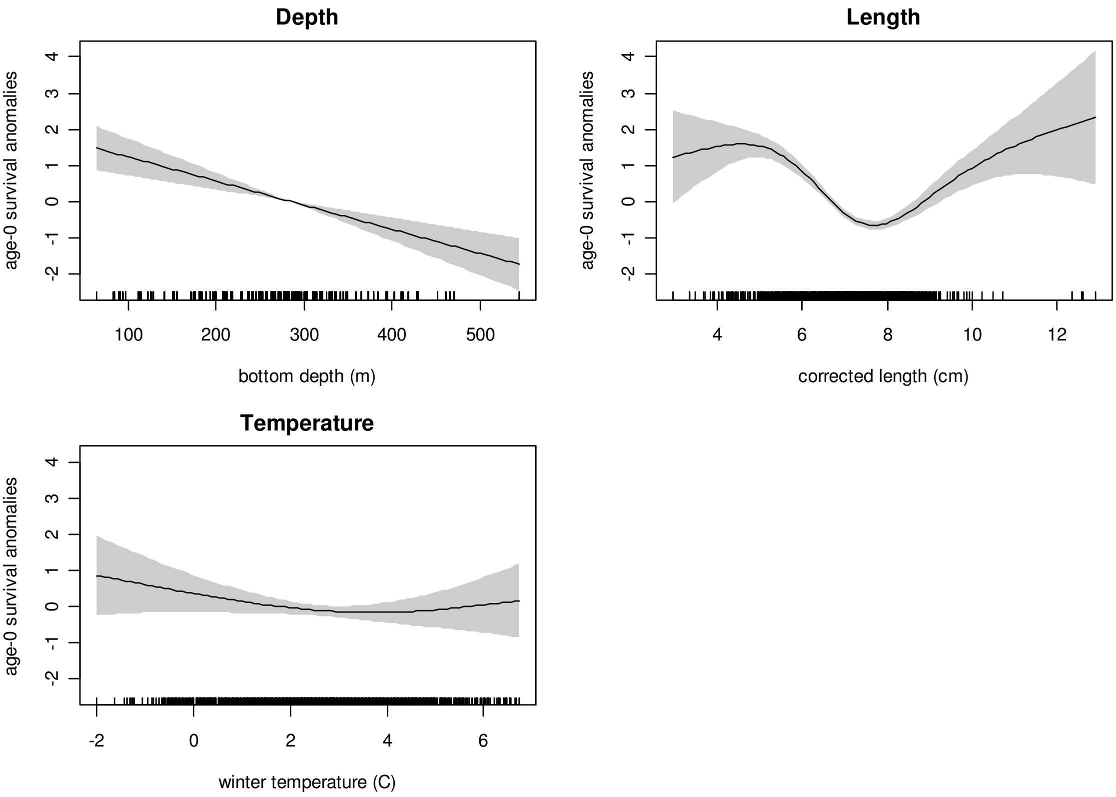

Figure 5 Effect of bottom depth, corrected age-0 length and winter bottom temperature on anomalies of age-0 cod survival, as predicted from the additive GAM model (see Eq. 2 in Methods). The shaded region indicates the 95% point-wise confidence interval and the rug along the x-axis indicate the location 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.

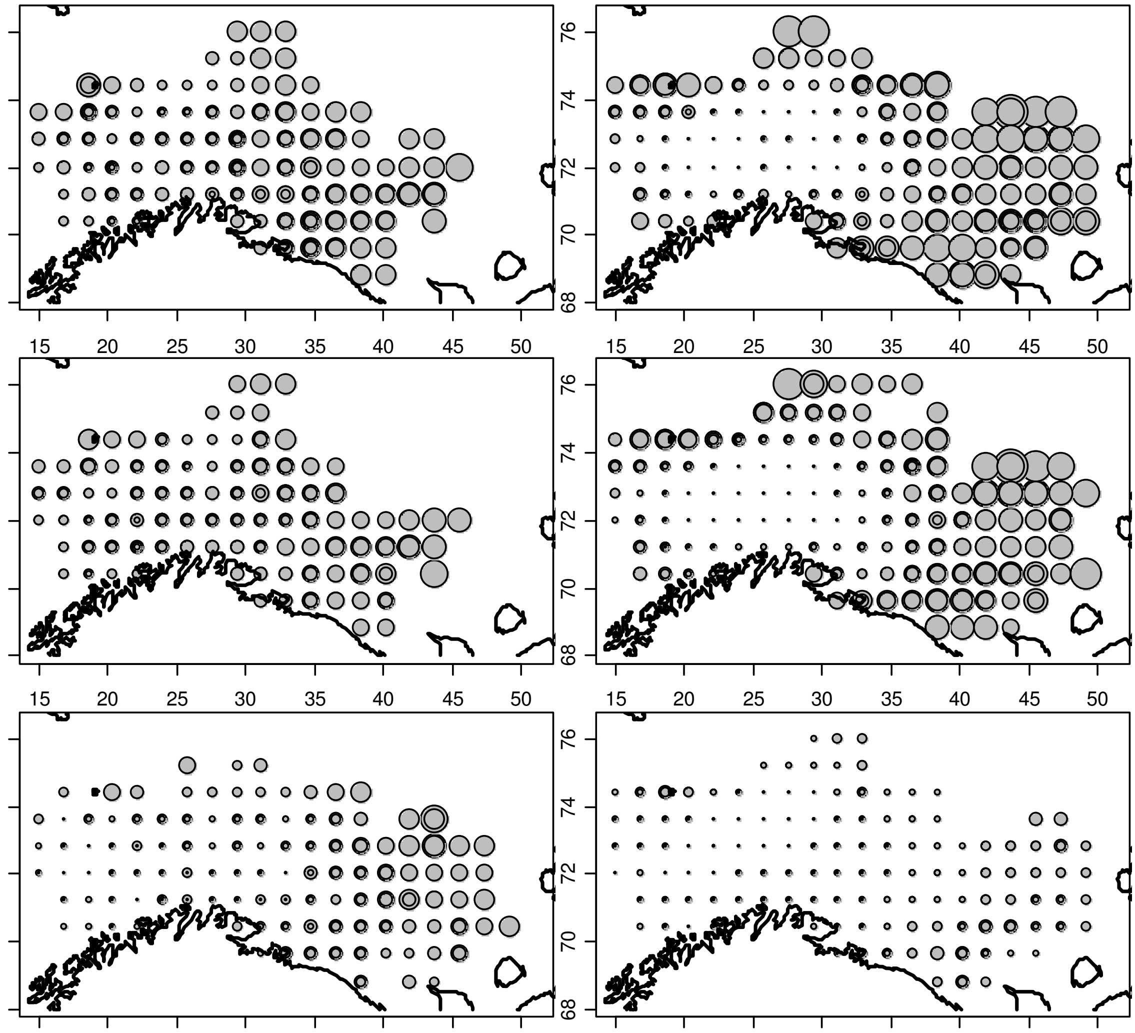

Figure 6 Spatial patterns of age-0 cod survival as predicted from the threshold GAM formulations (Methods: Eq. 3). Horizontal pairs of plots show the model predictions during a low (left) and high (right) regime, as defined by the following threshold biological variables: age-3+ cod biomass (first row); age-0 cod from fall survey (second row); harvest-corrected biomass of mature capelin (third row).

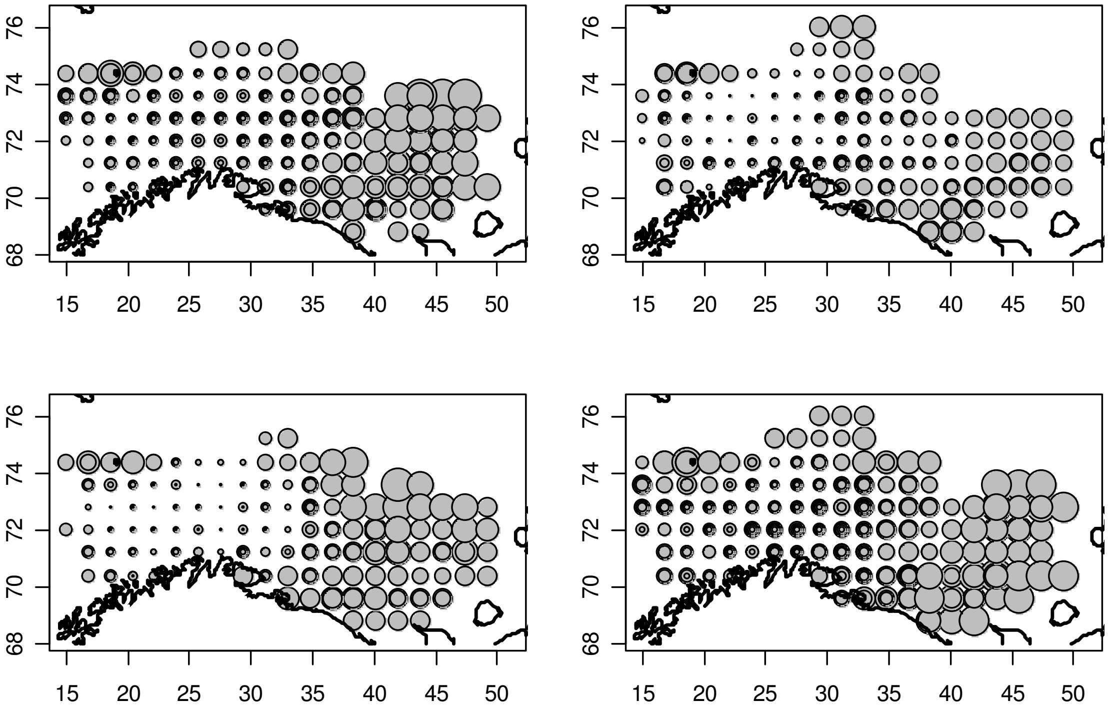

Figure 7 As in Fig. 6, for physical threshold variables. Threshold variables: winter Kola 0-200 m average water temperature (first row); Arctic Oscillation index (second row).

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 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.

Acknowledgements

LC was funded by an EU Marie Curie Intraeuropean fellowhips (FP-6); in addition CEES-core funding is acknowledged. Comments from Mėta Landys, improved earlier draft of the manuscript. The authors also acknowledge Edda Johannesen, Jan Erik Stiansen and Øyvin Strand for stimulating discussions and data gathering.

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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 ($s(\delta)$) 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.

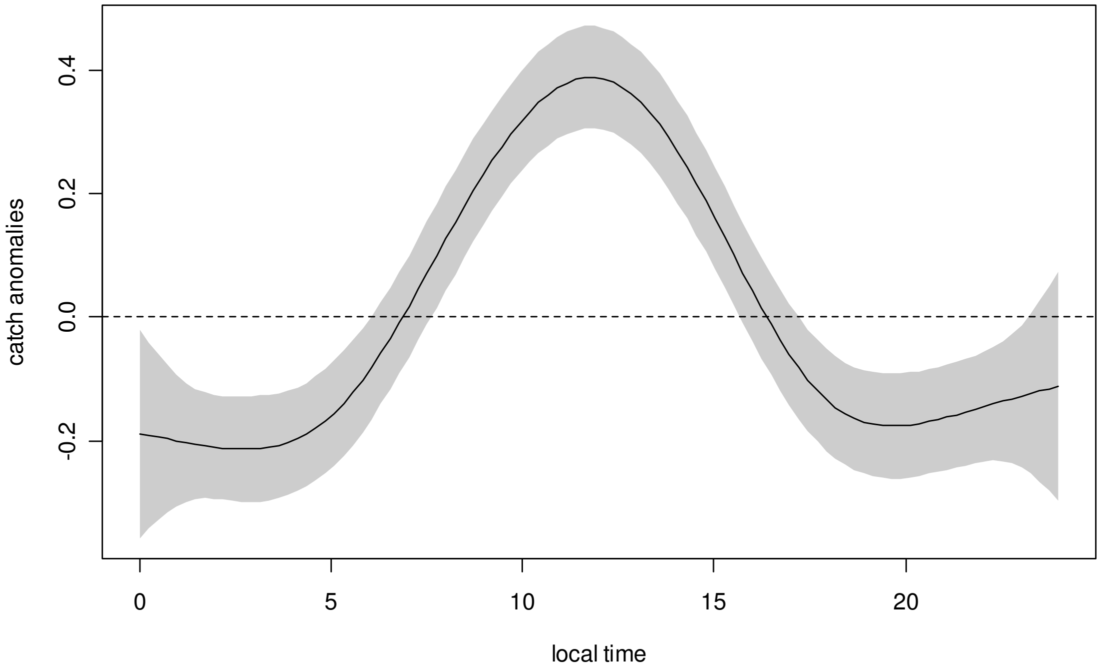

Figure A1 Anomalies in diel variability of log-transformed age-1 cod catches as predicted from a nonparametric model applied to the 1981-2004 surveys. Values above or below the dashed horizontal line respectively have a positive or a negative contribution on average cod catches. The shaded region indicates the 95% point-wise confidence interval. The average log-transformed cod catch was 5.72.

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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.

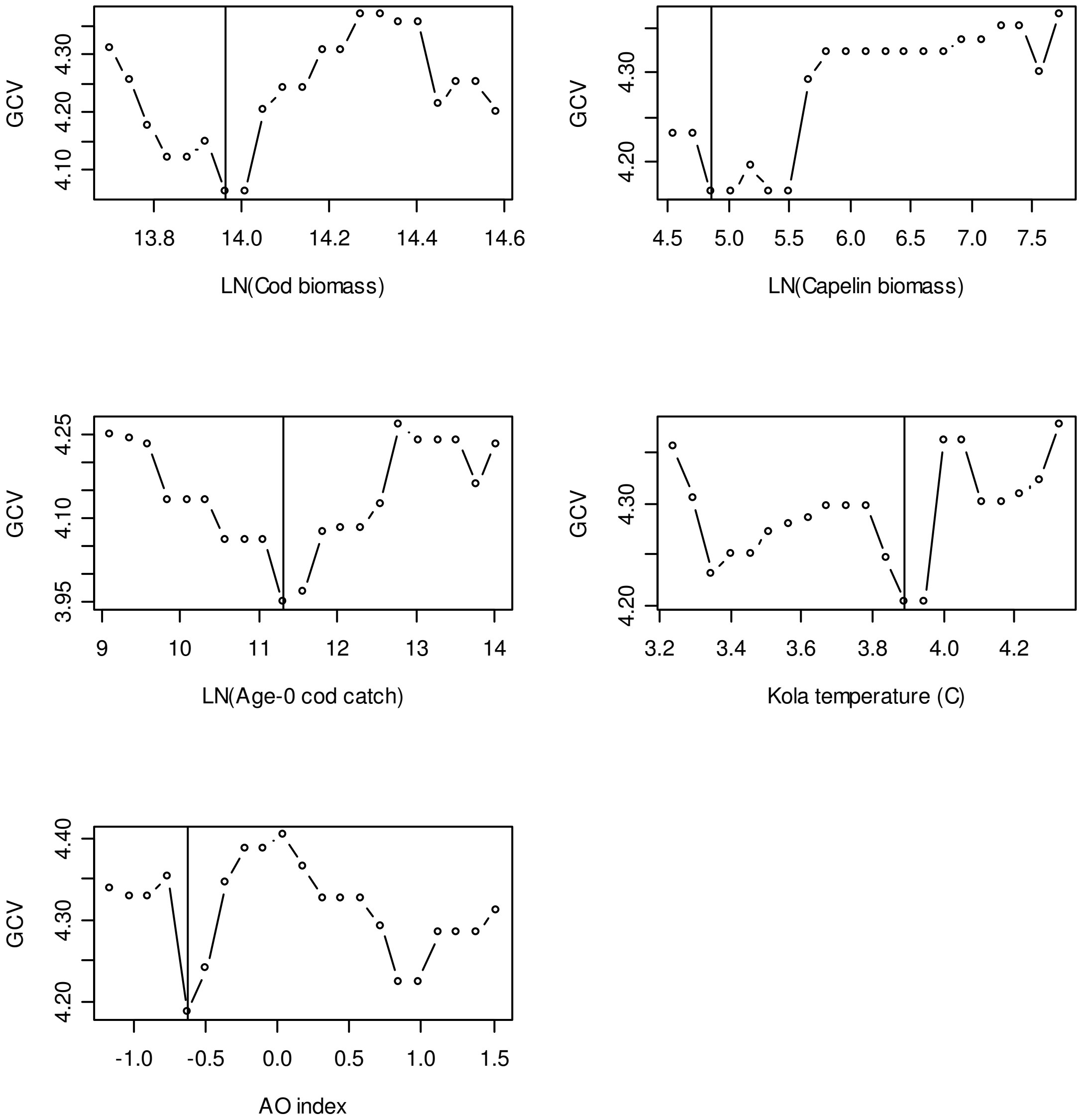

Figure B1 GCV profile for each of the examined threshold formulations. The vertical line indicates the selected threshold value.

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