SPATIAL ANATOMY OF SPECIES SURVIVAL: EFFECTS OF PREDATION AND CLIMATE-DRIVEN ENVIRONMENTAL VARIABILITY

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Abstract. 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 data from the Barents Sea, we study the spatiotemporal variability of the juvenile Atlantic cod (*Gadus morhua*) survival. We develop an index of spatial survival based on changes of juvenile cod distribution through their first winter of life (from age-0 to age-1) and study its variability in relation to biotic and abiotic factors. Over the 25 years analyzed (1980–2004), we found that, once the effect of passive drift due to dominant currents is accounted for, the area where age-0 cod survival was lowest coincided with the area of highest abundance of older cod. Within this critical region, the survival of age-0 cod was negatively affected by its own abundance, by that of older cod, and by bottom depth. Furthermore, during cold years, age-0 cod survival increased in the eastern and coldest portion of the examined area, which was typically avoided by older conspecifics. Based on these results we propose that within the examined area top-down mechanisms and predation-driven density dependence can strongly affect the spatial pattern of age-0 cod survival. Climate-related variables can also influence the spatial survival of age-0 cod by affecting their distribution and that of their predators. Results from these and similar studies, focusing on the spatial variability of survival rates, can be used to characterize species habitat quality of marine renewable resources.

Key words: Barents Sea; climate; cod; Gadus morhua; GAM; habitat quality; recruitment; spatial management; spatial survival.

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., Megrey et al. 1995, Quinn and Niebauer 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) factors 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. 2007) and thus may be

misrepresented when considered as an average over a spatial grid. It follows that an in-depth analysis of the processes 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.

Species–environment relationships are complex due to their possibly nonlinear and nonadditive nature. An extreme case of nonlinearity over space may take the form of a threshold response, resulting in a drastic rearrangement of species distribution following subtle changes in 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 25 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 prerecruitment dynamics, as individuals are confronted with a suite of survival challenges, such as settlement in a favorable environment, optimal pre-winter body condi-
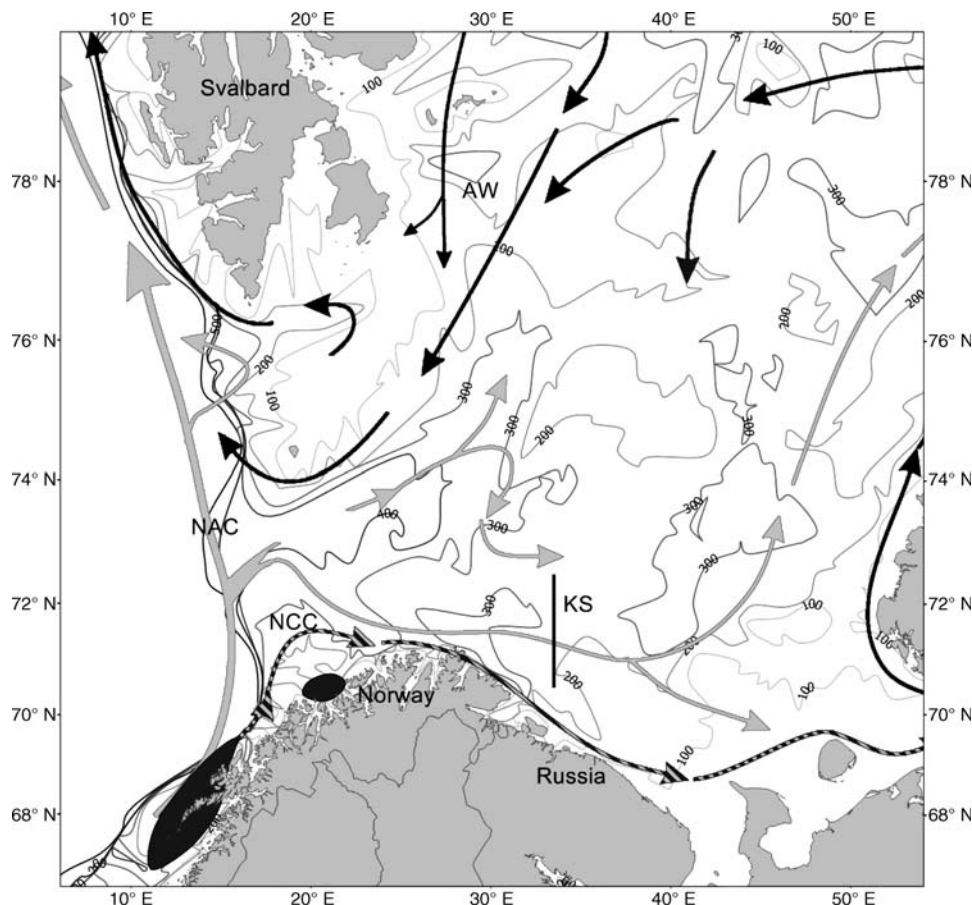
FIG. 1. The Barents Sea with depth contours and simplified current systems. NAC stands for North Atlantic Current, NCC for Norwegian Coastal Current, AW for Arctic Water, and KS for the Kola section. The dark shaded regions are main cod spawning areas.

tion 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.

The northeast 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 to seven years of age, migrate to the spawning grounds centered around the Vestfjorden and on the continental shelf outside Lofoten between 67°30′ N and 69° N (Fig. 1). 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 four to five months. Just before settlement, from late September and on, 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 (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.

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 (Institute of Marine Research/Polar Research Institute of Marine Fisheries and Oceanography 2005; from here on referred to as "fall survey"), and the 1981–2005 age-1 cod catches from the February–March bottom trawl survey (Jakobsen et al. 1997; from here on 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 square nautical mile and number per nautical miles trawled, respectively. From here on, 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 (Institute of Marine Research/Polar Research Institute of Marine Fisheries and Oceanography 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. From 1989 onward, 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).

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). Water temperature was measured both during the fall survey (T_F) as the average over the 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 (L. Ciannelli, *personal observation*). Thus, using the relationship between size and day of capture, we referred individual lengths to the median date of the fall survey.

Other covariates included in the analysis, in the form of annual averages, are (1) surface to bottom average horizontal current velocity (m/s) along the 30° longitude line running from the coast to 77° of latitude north.

Current values, as monthly averages, were predicted from the ocean circulation model described in Budgell (2005). Only values during the months of August and September were considered, i.e., when age-0 cod are still in their pelagic phase. (2) Natural logarithm of the annual cod biomass (from age-3 onward; International Council for the Exploration of the Sea 2005). (3) Age-0 cod availability, calculated as the residuals from the linear regressions between the logarithm of annual cod biomass and the logarithm of the annual age-0 cod abundance estimated from the fall survey. Age-0 and adult cod abundances were to some degree linearly correlated ($R^2 = 49\%$), thus the use of residuals removed the correlation problem while retaining information on age-0 abundance in relation to that of adult cod (i.e., availability). (4) Winter Barents Sea thermal index as an average from December to March of the 0–200 m water temperature along the Kola section (Fig. 1; Bochkov 1982, Tereshchenko 1996; values for later years kindly provided by Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia).

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° to 76.8° N and from 15.0° to 51.0° E, with increments of 0.8° and 1.8° in the latitude and longitude direction, respectively. The range and resolution of the grid matched those of the winter survey. At each grid point, age-0 and age-1 cod catches and the co-located covariates were derived as the average within a circle of radius (d) equal to 75% of the shortest distance between two grid points in the longitude direction. In establishing the length of d we tried to achieve a balance between the contrasting needs of reducing the overlap between two neighboring 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 northern and southernmost 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, and φ and λ are degrees of longitude east and latitude north, respectively. Note that this index is equally affected by both the actual local survival of age-0 cod and by their movement. We realize that when referring to the index in Eq. 1, the use of the term spatial survival can be misleading, as it places an emphasis on survival rather than movement processes. However, as

explained in greater details in the remainder of the methods section (see in particular Eq. 3), we account for potential sources of movement when studying the spatial variability of the metric in Eq. 1.

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, Wood 2006). We implemented two types of GAM formulations: (1) 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 (2) threshold, where the effect of location changes in relation to external threshold variables. The additive formulation is

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

where s and g respectively are two-dimensional (thin-plate regression spline; Wood 2003) and one-dimensional (natural cubic splines; Wood 2004) smoothing functions, D is the bottom depth, L 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 $\varepsilon_{(\varphi,\lambda)}$ is a normally distributed error term. The covariate selection strategy was based on the generalized cross validation (GCV), a measure of the model predictive squared error (Green and Silverman 1994). In particular, a covariate was retained in the model if its removal caused an increase of the GCV (Wood 2000).

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 values of one or more external environmental variables (E). This additional feature of the analysis is essential to assess the nonlinear and possibly threshold effect of contrasting environmental and climatic regimes. Specifically,

$$S_{t,(\varphi,\lambda)} = k_g + g_1\left[D_{(\varphi,\lambda)}\right] + g_2\left[T_{(\varphi,\lambda)}\right] + g_3\left[L_{(\varphi,\lambda)}\right] + \varepsilon_{(\varphi,\lambda)}$$
$$+ \begin{cases} k_1 + s_1(\varphi,\lambda) & \text{if } E_t \leq r \\ k_2 + s_2(\varphi,\lambda) & \text{if } E_t > r. \end{cases} \qquad (3)$$

The environmental variable E is used to partition 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 restricted range of the covariate E (Ciannelli et al. 2004; Appendix B). The range was restricted to the upper 0.8 and lower 0.2 quantiles to guarantee that at least 20% of the available sample size is included in a single regime. In 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. Note that the extension of the model in (3) to more than two regimes, defined for example by all possible combinations of two environmental threshold variables, can be readily achieved by introducing a new intercept and position effect for each of the scrutinized regime.

We ran four versions of the model in Eq. 3, each with a different threshold variable E, including (1) horizontal current velocity along the 30° longitude line; (2) natural logarithm of the annual cod biomass; (3) age-0 cod availability; and (4) December to March average water temperature along the Kola section. Models were compared based on their genuine cross validation (CV; Appendix B). Each of the threshold variables were included in the analysis for its potential to affect the survival metrics of age-0 cod, either directly via changes of current or predation intensity, or indirectly via changes of climate-driven environmental conditions (Kola water temperature).

Movement can be an important source of variability of the survival metrics. We assume that passive drift during the months of August and September is the dominant source of young cod movement. If there was an effect of the current on age-0 cod spatial survival, the additional threshold formulations were applied to each current regime. For example, if we were interested in assessing the effect of cod biomass during both low and high current regimes, we would formulate a model with the following four terms: (1) low cod–low current, (2) high cod–low current, (3) low cod–high current, and (4) high cod–high current. In this particular case, the current threshold would be constant at the previously estimated value, while the cod threshold would be estimated anew.

RESULTS

Average distribution of water temperature and juvenile catches

Both fall and winter water temperatures were on average highest toward the southwest corner 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° N and from about 20° to 35° E (Fig. 2). Catches sharply declined to the west, corresponding with 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
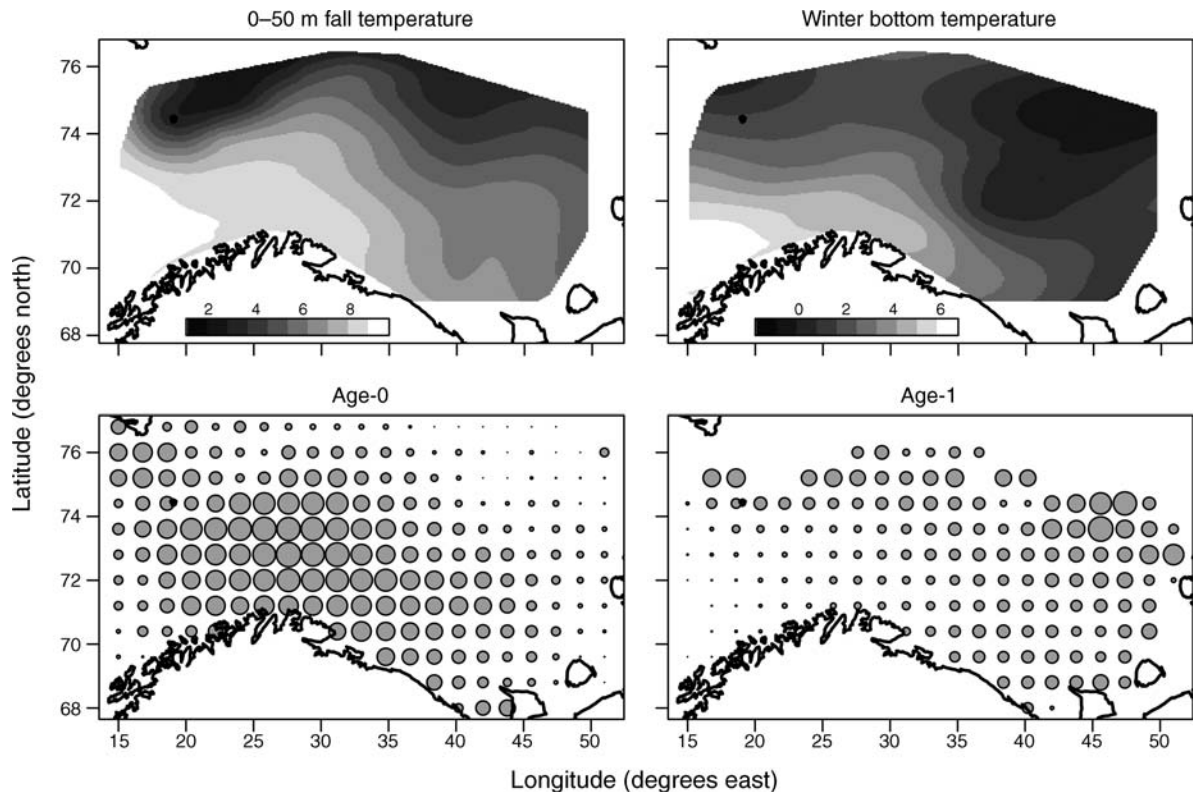
FIG. 2. Average distribution of 0–50 m average fall water temperature (top left), winter bottom temperature (top right), and age-0 (bottom left) and age-1 (bottom right) cod standardized catches. The area of the circles in the lower two panels is proportional to the log-transformed and effort-standardized 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 westernmost edge of the grid and toward the shelf break (Fig. 2).

Spatial survival of age-0 cod

Based on the predictions of the additive GAM formulation (Eq. 2), the area where age-0 cod experience the lowest survival (referred to as "critical area") was bounded by the Norwegian coastline to the south, by 30° longitude to the east and by 74° latitude to the north (Fig. 3). Throughout the examined grid, age-0 survival was negatively correlated with bottom depth and with winter water temperature up to about 3°C, and positively above that value. The effect of length was U-shaped with a minimum at about 7–9 cm (Fig. 3).

Results from the threshold GAM formulations (Eq. 3) clearly indicate that, within the examined region, the index of 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, the survival index increased to the east when the eastward current velocity was high (Fig. 4). This expected result indicates that passive drift can affect the spatial distribution of age-0 cod through fall. However, the additional partition of the age-0 survival patterns in relation to the other examined

threshold covariate, further improved the model results, both in term of explained variance and model CV. Age-0 cod survival was considerably reduced throughout the critical area (Figs. 5 and 6) and as an average value throughout the sampled grid (Table 1) during years characterized by high adult cod and high age-0 cod availability, regardless of the current regime. In contrast, when adult cod abundance and age-0 cod availability were low, age-0 cod survival was nearly constant throughout the sampled grid only when the current was also low, otherwise it increased to the east (Figs. 5 and 6).

When Kola temperature was used as a threshold, survival of age-0 cod increased to the east when current velocity was high, but to a lower extent, also when temperature was low (Fig. 7). The threshold (3.30°C) coincided to the lowest value of restricted Kola temperature range (Appendix B). The lack of a minimum closer to the center of the range may indicate a gradually changing effect of Kola temperature on age-0 survival, rather than a threshold one. Due to the extreme value of the selected threshold, there were not enough samples to the east to compare survival values during years with high current and low Kola temperature with those of other inspected regimes (Fig. 7).
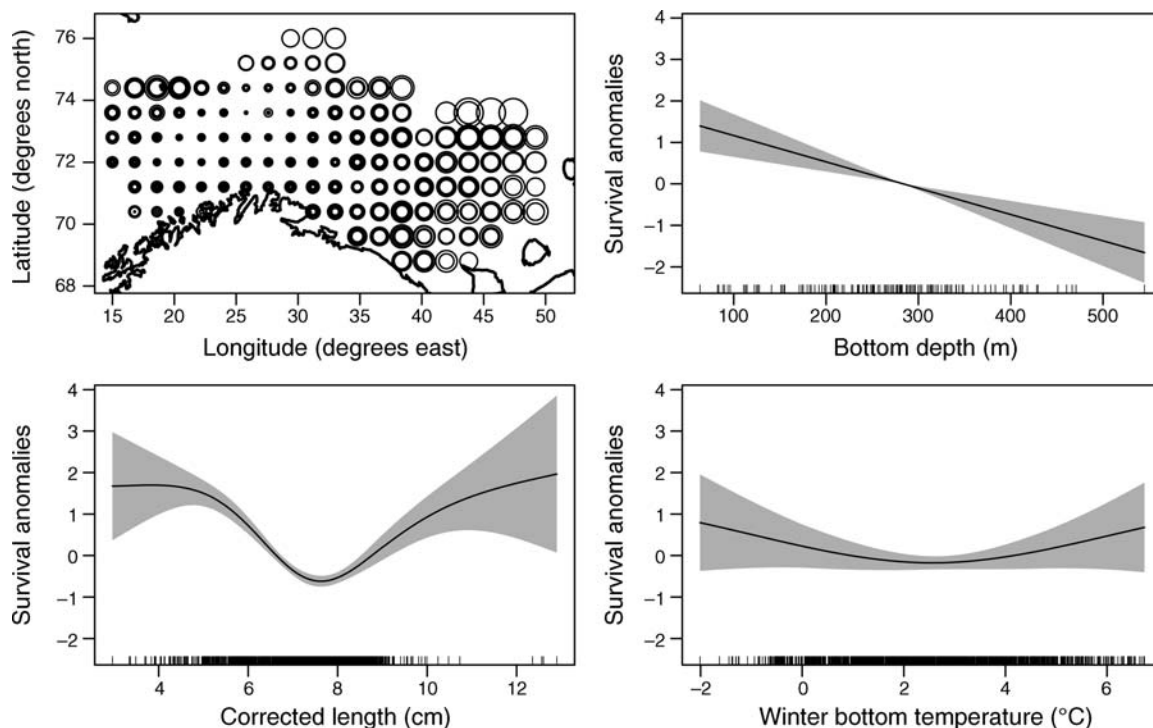
FIG. 3. Top left: spatial patterns of age-0 cod survival from 1980 to 2004 as estimated by an additive generalized additive model (GAM) including geographic coordinates (latitude and longitude), bottom depth, fish length, and winter temperature as covariates (see Eq. 2). Circle size is proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metric. The remaining three plots show the effects of bottom depth, corrected age-0 length, and winter bottom temperature on anomalies of age-0 cod survival. The shaded region indicates the 95% point-wise confidence interval, and the rug along the x-axis indicate the location of the observations.

However, the results from a marginally inferior model (in term of GCV), and with a slightly higher temperature threshold (i.e., 3.54°C), indicated that when the current velocity was high, there were no visible differences of age-0 survival to the east between years of high and low Kola values (Appendix B).

The center of older cod (>35 cm length) distribution coincided with the estimated critical area of age-0 cod survival (cf. Figs. 3 and 8). Moreover, during years characterized by high Kola temperature, older cod distribution increased to the east, in correspondence of the area where age-0 cod experienced lower survival.

The estimated threshold for each of the threshold models fell close to the median value of the examined covariate range, except for the Kola model where the threshold coincided with the lowest extreme (Appendix B). In all examined threshold GAM formulations, the effect of the other co-located covariates was similar to the one already described for the additive model (Fig. 3). Some differences were found when adult cod and Kola temperature (in addition to current) were used as a threshold variable. In the former, winter temperature had a slightly positive effect throughout its range, while in the latter fall rather than winter temperature was selected. The effect of fall temperature was also negative. From a visual assessment, none of the residual patterns

from the inspected models presented signs of heteroscedasticity or had strong departure from normality.

DISCUSSION

Our analysis 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. The full extent of these spatial survival dynamics, detected through changes in young cod distribution through their first winter of life, can be masked by the passive drift that individuals undergo prior to settling. However, we also found that passive drift alone was not sufficient to explain the entire range of young cod survival variability. For example, by simple back of the envelope calculations, the average distance that age-0 cod could potentially drift (115 km), given the incumbent flow regime during the months of August and September (average velocity of 0.02 m/s over a period of two months), is considerably less than half of the average distance separating the centers of age-0 and age-1 cod distributions (304 km). In accordance, we found that other variables, related to predation, are very important in explaining young cod changes in distribution through fall and winter. The inclusion of both passive drift and these other variables
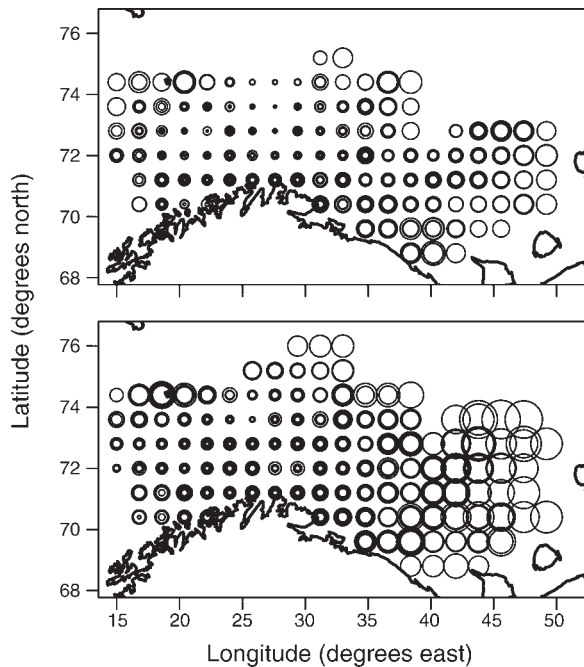
FIG. 4. Spatial patterns of age-0 cod survival as predicted from the threshold GAM formulations (Eq. 3) during low (top) and high (bottom) eastward current velocity regimes. Circle sizes are proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metrics.

has greatly improved the models both in term of explained variance (from about 37% to 50%) and CV (from 4.59 to 3.99) and has augmented our understanding of how juvenile cod survive and distribute in the Barents Sea through their first winter of life.

The most remarkable changes of age-0 cod survival, once those due to flow regime were accounted for, were found in relation to older cod abundance and to age-0 cod availability—a result that underscores the significance of predation. 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 between the critical area of age-0 cod survival and the distribution range of older cod, particularly during warm environmental regimes.

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. (2007) 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
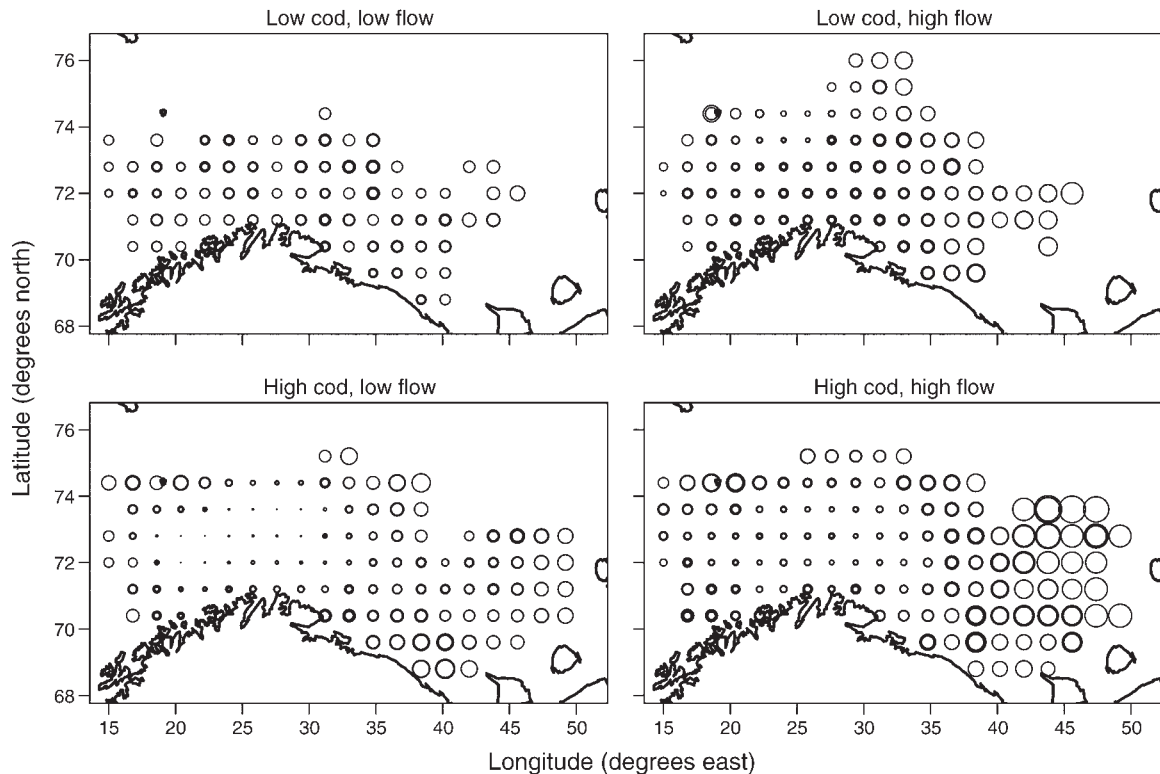

FIG. 5. Spatial pattern of age-0 cod survival over four environmental regimes, defined by average current velocity and by adult cod abundance. Circle sizes are proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metrics.
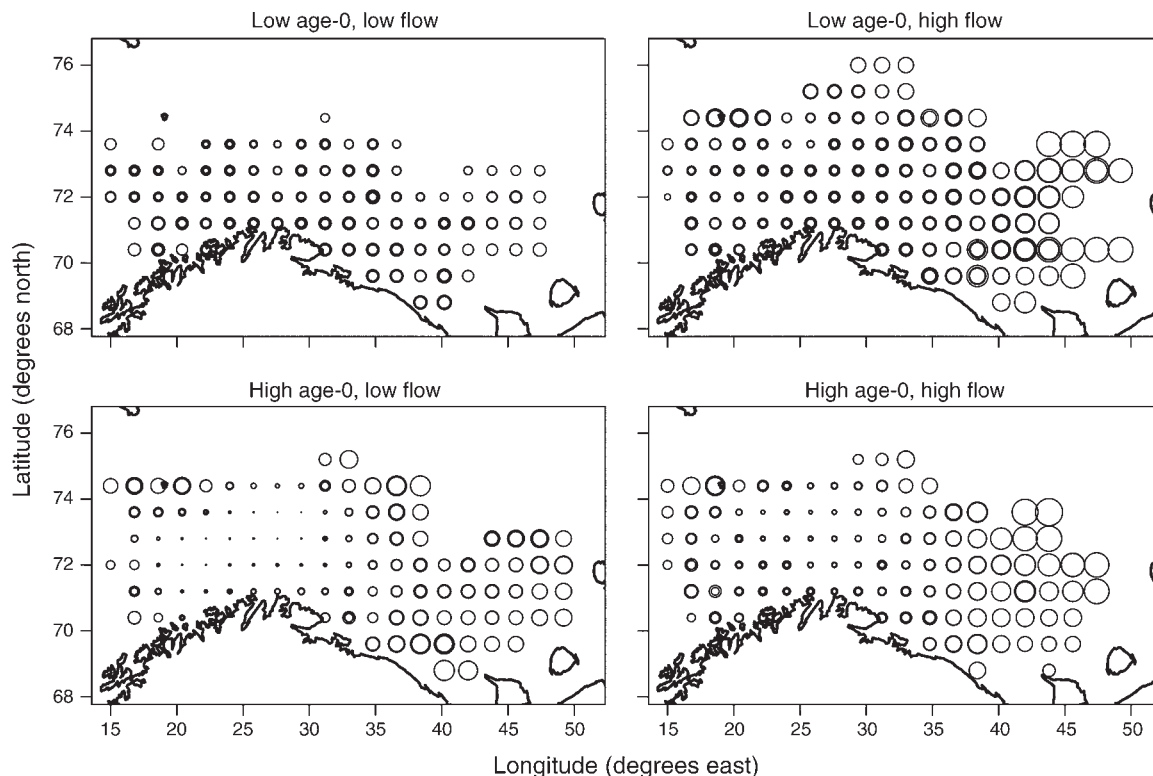
FIG. 6. Spatial pattern of age-0 cod survival over four environmental regimes, defined by current velocity and by the residuals of a linear model between average age-0 and adult cod abundance. Circle sizes are proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metrics.

years, age-0 cod survival was reduced also in the easternmost range of the examined region. However, such an effect was detectable only during years of low eastward current velocity. Older cod tend to reside in warmer waters during winter compared to juveniles (Ottersen et al. 1998), and as also shown here (Fig. 8), they may expand their distribution range to the east during warm years (Nakken and Raknes 1987). Such an eastward expansion increases the spatial overlap and

consumption of the eastward displaced and newly settled juveniles. In contrast, during years characterized by both high Kola temperature and high current velocities, the effect of predation on easterly displaced fish may be subordinate to that of eastward current flow, and therefore not detectable. In our winter data set age-1 cod were caught in waters with bottom temperature well below 0°C while older cod avoided those areas, probably indicating a lower tolerance of the latter

TABLE 1. Summary of the model results for each of the formulations examined.

Parameter	Additive	Threshold flow	Threshold flow, cod	Threshold flow, age-0	Threshold flow, Kola
R^2	37.0	44.1	48.2	48.9	49.5
Genuine cross validation	4.59	4.15	3.99	4.04	3.99
Th (SD)	NA	0.02 (0.00)	13.94 (0.05)	0.35 (0.39)	3.30 (0.02)
Th-range	NA	0.02–0.02	13.81–14.28	−1.11–0.39	3.30–3.35
K_1 (SE)	NA	−8.83 (0.12)	−8.10 (0.16)	−8.69 (0.13)	−9.06 (0.16)
K_2 (SE)	NA	−7.62 (0.10)	−7.72 (0.11)	−7.62 (0.08)	−8.47 (0.17)
K_3 (SE)	NA	NA	−9.21 (0.09)	−9.19 (0.11)	−9.00 (0.10)
K_4 (SE)	NA	NA	−7.92 (0.10)	−7.94 (0.11)	−7.56 (0.09)
N	1406	1406	1406	1406	1256

Notes: The coefficients $K_{1–4}$ indicate the average value and the standard error (SE) of age-0 cod survival throughout the inspected region, during the environmental regimes defined by the current velocity (m/s) and by the additional environmental variable (E) specified in the column heading. The order is the following: (1) low flow and low E, (2) high flow and low E, (3) low flow and high E, (4) high flow and high E. Note that the additive model formulation does not have any regime-dependent survival coefficient and that the model formulation with flow as a threshold variable has only two regime dependent coefficients (i.e., low and high flow, respectively). Th (SD) is the estimated threshold value and standard deviation from cross-validation; Th-range is the estimated range of threshold values from cross validation; N is sample size; NA, not applicable.
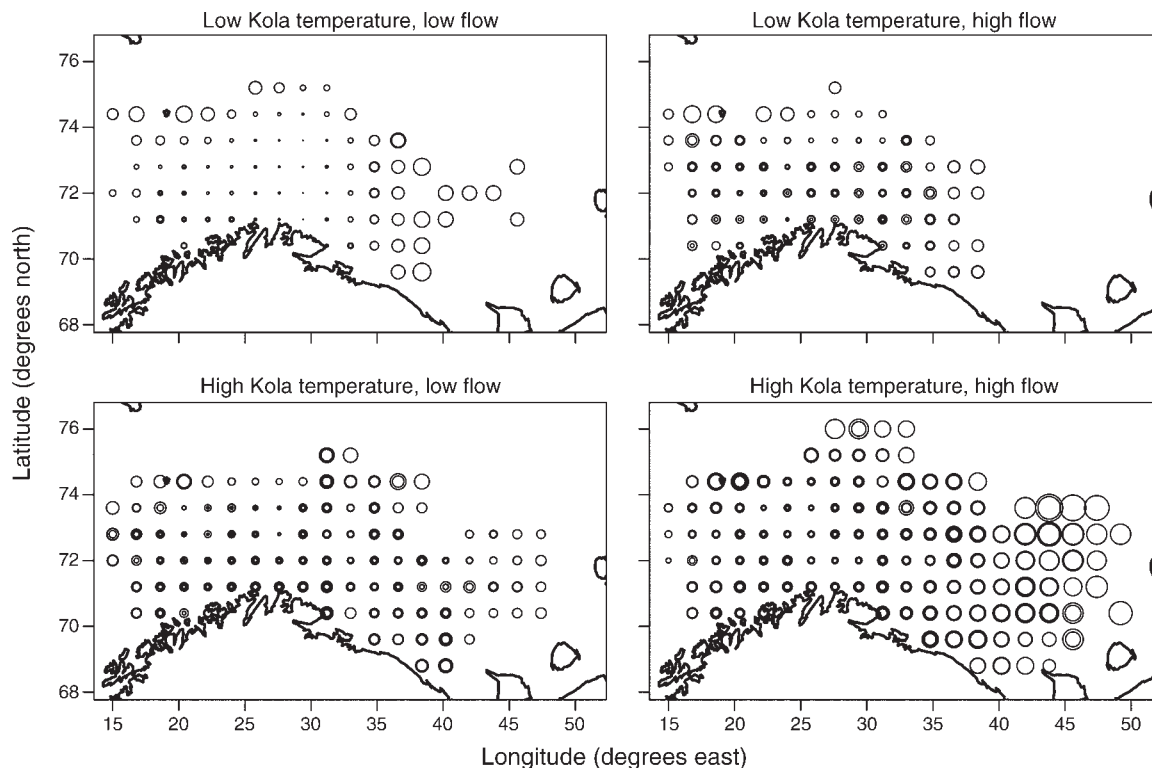
Fig. 7.　Spatial pattern of age-0 cod survival over four environmental regimes, defined by current velocity and by the water temperature along the Kola section. Circle sizes are proportional to the survival metrics. Circles of different sizes within the same grid location reflect the interannual variability of the survival metrics.

toward extremely low temperatures. Studies in the northwest Atlantic 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).

The spatial pattern of age-0 cod survival was negatively correlated with co-located depth, and non-linearly related with winter water temperature and age-0 length. We believe that the effect of depth was the consequence of volitional 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 effect of co-located water temperature, although limited compared to that of other covariates, indicates an increase of age-0 survival particularly at very cold temperature extremes (i.e., <0°C). Both fall 0-50 m and winter bottom water temperature 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 due to lower temperatures (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.

Our analysis presented 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.
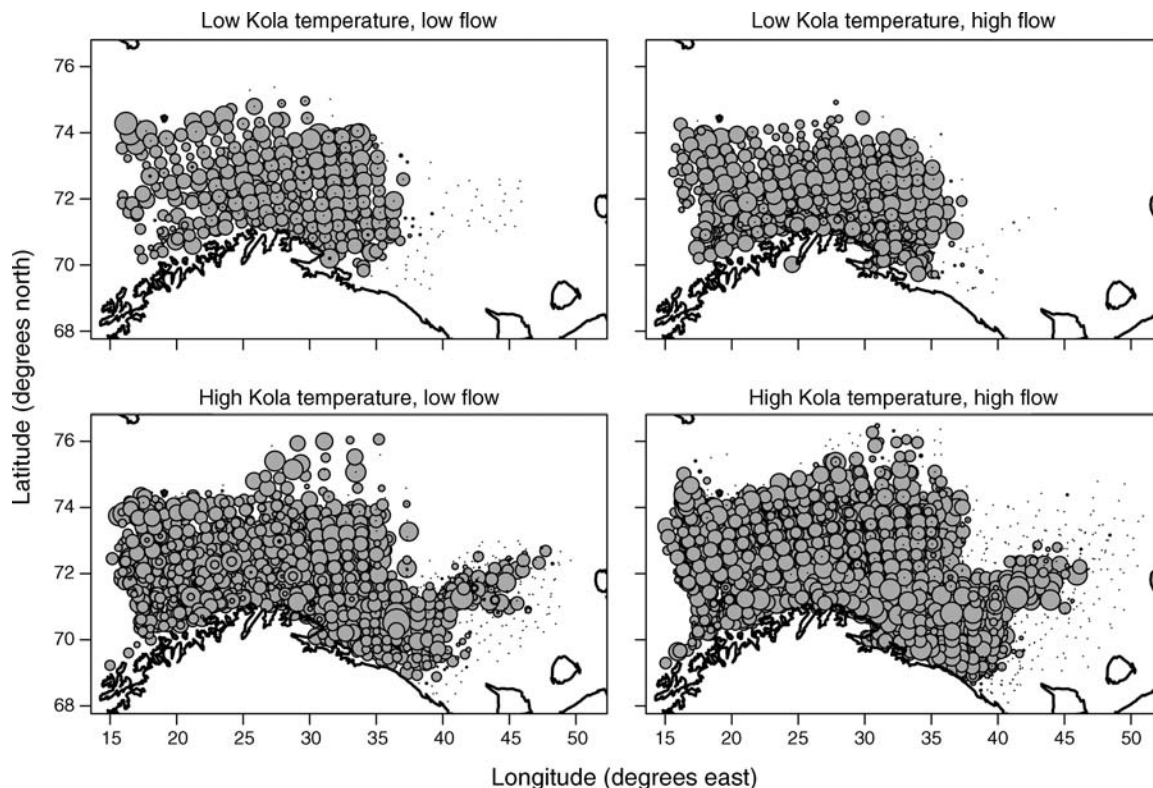
F_IG. 8.   Distribution of adult cod from the winter bottom trawl survey, partitioned according to water temperature along the Kola section and to the average current velocity along the 30° longitude line. The environmental regimes are the same as the one estimated in the age-0 survival analysis shown in Fig. 7. The area of the circles is proportional to the log-transformed and effort-standardized catches. Dots indicate stations with zero catch.

Second, part of the age-0 cohort will have settled before the survey, and therefore will be less vulnerable to the midwater sampling gear. 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. To date, the issue of age-0 cod settlement in the Barents Sea is not fully clarified. Observations indicate that bottom settling starts about at the time of the 0-group survey, and considerably less 0-group are found in upper layers in the second half of September compared to the first half of September. Data from the Russian bottom trawl survey in October-December indicate that the bottom settling process is finished by then (Lepesevich and Shevelev 1997). 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.

Understanding the spatial pattern of species survival is critical toward their management. In marine ecology there is an increasing awareness of the need for 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 (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), 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 a 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 local survival. The case illustrated for age-0 cod in the Barents Sea is very elucidating: the area typically corresponding to the highest 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.

In the Barents Sea, age-0 and age-1 cod are not caught in directed fisheries, but to some extent are caught as by-catch in shrimp (Pandalus borealis) fisheries. The shrimp fisheries are continuously monitored, and if the by-catch is too large (the limit is at present eight specimens of cod

per 10 kg shrimp), the area is closed to shrimp fisheries. This regulation seems to function well, as the estimated by-catches in recent years are very small and negligible compared to estimates of cod cannibalism (International Council for the Exploration of the Sea 2006). Thus, current management practices based on area restriction already minimize by-catches of young cod. 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 in understanding the joint effects of spatial and temporal environmental variability on species distribution and survival, under incumbent climate and environmental changes.

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APPENDIX A

Adjustment for diel variability of age-1 cod catches (*Ecological Archives* E088-043-A1).

APPENDIX B

Selection of threshold values (*Ecological Archives* E088-043-A2).