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Spatial patterns of age-0 cod survival in the Barents Sea

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Abstract
Apart from human harvest, recruitment dynamics is conceivably recognized as the main source of population variability of marine fish stocks. Factors affecting recruitment dynamics can change over both temporal and spatial scales. It follows that at the same time, over the entire range of distribution of a single population, different individuals may experience different level of environmental forcing and survival, which may not be well represented by average conditions throughout the entire distribution range. In this study we focus on the spatial pattern and its relative sources of variability in the survival of the Arcto-Norwegian cod (*Gadus morhua* L.) from the age-0 to the age-1 stage. This is a delicate phase of the cod pre-recruitment dynamics, as individuals are confronted with a suite of survival challenges, such as settlement, pre-winter body condition, growth, and predation avoidance. During the over 20 years analyzed (1980-2004), we found that on average age-0 cod experience lower survival in the areas north of the Norwegian coastline, from about 71 to 75 degree of latitude north and about 20 to 35 degree of longitude east. However, in coastal areas, immediately north of the Norwegian coastline, age-0 cod experience greater survival. Within the studied area, the average survival of age-0 cod is significantly greater during years with low adult cod and high capelin abundance, and high Arctic Oscillation. In addition, when capelin abundance is high, age-0 cod experience better survival particularly near the Norwegian coastline. Based on these results it appears that within the sampled grid the observed geographic patterns of age-0 cod survival is affected by the predation from adult cod in relation to the availability and distribution of capelin (*Mallotus villosus*), the alternative and preferred prey of adult cod. Climate can affect the spatial survival of age-0 cod by both affecting the distribution of their predators (e.g., adult cod) and the distribution and availability of zooplankton prey.

Introduction

In this study we are interested in the interactions between spatial and temporal dynamics in the survival of the juvenile stages of the Arcto-Norwegian (also known as North-east Arctic or Barents Sea) cod (*Gadus morhua* L.). This stock of cod spawns along a 1200 km coastline from mid to north Norway. 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 in November-February (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 and start to become more demersal. Just before settlement their spatial extension reaches its maximum (Sundby et al. 1989), extending 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 (*Mallotus villosus*), their preferred prey, they start to follow their migration towards the coasts of Russia and northern Norway in winter, and north and eastwards during summer.

Our focus is on survival during the first autumn/winter of the cod life cycle (i.e. from September to February). This is a delicate phase of the cod pre-recruitment dynamics, as young cod are confronted with a suite of survival challenges, such as settlement, pre-winter body condition and growth, and predation avoidance. In the first part of the study we derive a spatially-explicit index of age-0 cod survival, which allows us to identify regions with poor (high) survival, within the sampled grid. Subsequently, using nonparametric regression analysis (i.e. generalized additive models, GAM) we seek to identify the causes behind the formation of the observed geographic survival pattern. This we do by correlating the spatial index of age-0 cod survival with the environmental covariate typical of the examined location, and by studying patterns in survival distribution over different regimes of climate (Arctic Oscillation), predator (adult cod) and alternative prey (capelin) availability. To our knowledge this is the first study that explicitly addresses the spatial variability in the survival of a large marine fish population. We believe that results from this and similar studies are sorely needed to better include spatial consideration in the management of marine renewable resources.

Methods

The data

The data used in the analysis include age-0 cod catches from the summer-fall (August-September) midwater trawl survey (Anon. 2005), and age-1 cod catches from the winter (February) bottom trawl survey (Jakobsen et al. 1997). The two stages considered in this study are separated by about 5 months of life. 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 did also change in the early 1980s (Dingsør 2005). Age-0 cod catches were adjusted for gear catchability in relation to fish length, being the larger age-0s typically more vulnerable to the sampling gear (Anon. 2005). The catch of age-1 individuals was derived from the total bottom trawl catches based on age-length keys varying by sampling sub-area and year surveyed, and it included fish ranging in length from 5 to 24 cm. After 1993 the net used in the bottom trawl survey was lined with smaller mesh codend, which significantly affected the catch of younger cod. To account for this change in sampling methodology we included a gear factor in our models of spatial age-0 survival (see below). Age-0 and age-1 cod catches were standardized by effort, and expressed as no. per nm^2 and no. 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.

Definition of age-0 cod spatial survival

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 cohort as follows:

$$S_{t,(\varphi,\lambda),d} = \overline{x'_{t,1,d}} - \overline{x_{(t-1),0,d}} \quad (1)$$

where $\overline{x_{(t-1),0,d}}$ and $\overline{x'_{t,1,d}}$ are the natural logarithm of the average density of age-0 and *corrected* age-1 cod respectively, within a circle centred in φ degree of longitude east and λ degree of latitude north and radius equal to *d*. The value of *d* was fixed to 100 km, as a balance between the opposing need to account for fish movement during the approximately five months separating the two surveys, and to preserve spatial differences in fish survival over the entire sampling grid. We corrected the bottom trawl catches of age-1 cod for the bias introduced by diel vertical migrations. The formula in (1) was applied to all stations sampled during the winter bottom trawl survey.

Analysis of spatial patterns in age-0 cod survival

Spatial patterns of age-0 cod survival were investigated with GAM models, applied to the entire spatio-temporal set of survival data. In addition to the additive formulation which assumes no interannual variation of distribution in age-0 survival (except that due to the change of gear), we applied a nonadditive formulation, in which the effect of position on the distribution of age-0 cod survival and the average survival level are allowed to change according to the level of an external environmental threshold variable The procedure applied for the nonadditive model analysis is illustrated in Ciannelli et al. (2004). In the current analysis we tested the effect of four different threshold variables: average annual cod biomass (from age-3 onward, natural log transformed; ICES 2005), natural log of the annual mature capelin biomass in October (ICES 2005; see Gjøsæter et al. 1998 for capelin assessment methodology), the ratio of cod and capelin log-transformed biomasses, and finally, the monthly Arctic Oscillation index averaged from (AO) from December to March (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). Each of the chosen threshold variables was included in the analysis for their potential to affect the spatial survival of age-0 cod, either directly via changes of predation intensity or growth of young cod (e.g. cod biomass and climate index, respectively) or indirectly via the presence of alternative prey or the relative distribution and overlap of between predator and prey (e.g. capelin and climate index, respectively).

Results

The additive model of age-0 cod spatial survival explained 39.0% of the spatio-temporal variability. Based on the model predictions, the area north of the Norwegian coastline, from about 71 to 75 degree of latitude north and about 20 to 35 degree of longitude east was the one with the lowest values of age-0 cod survival (Fig. 2). However, in the immediate vicinity of the Norwegian coastline, age-0 cod survival increased. Age-0 cod experienced the greatest survival in the easternmost portion of the sampled winter grid (Fig. 2).

The inclusion of annual cod biomass as a threshold variable of the position effect (nonadditive formulation) considerably improved the model fit and predictive error. The model results indicated that during years with low cod biomass, age-0 survival is on average 30% higher than in years with high cod biomass. The spatial results also support the evidence of lower survival during high cod regimes (Fig. 3).

The next best model was obtained by including the AO index as a threshold variable. Specifically, during years with high AO, on average age-0 cod experienced better survival and an overall increase of spatial survival throughout the sampled grid, but particularly in the areas close to the north-western portion of the Norwegian coastline (Fig. 4). A model partitioned with the ratio between the adult cod and mature capelin biomasses also produced better results than a fully additive model. Expectedly, during low cod and high capelin years, age-0 cod experience greater survival, particularly north of the Norwegian coastline.

Discussion

The results of our analysis support the following points:
1) age-0 cod experience very low survival in the areas north of the Norwegian coastline, from about 71 to 75 degree of latitude north and about 20 to 35 degree of longitude east. However, in coastal areas, immediately north of the Norwegian coastline, age-0 cod experience greater survival (Fig. 2).
2) Within the sampled grid of the winter survey, the average survival of age-0 cod is significantly greater during years characterized by high AO index, low adult cod and high capelin biomass.
3) The geographic distribution of age-0 cod survival also changes according to the abundance level of adult cod and capelin. When cod abundance is low age-0 cod experience greater survival throughout the critical areas identified in Fig. 2. When capelin abundance is high in relation to adult cod biomass, age-0 cod experience better survival particularly near the Norwegian coastline.

Based on these results it appears that within the sampled grid the observed geographic patterns of age-0 cod survival is driven by the predation from adult cod in relation to the availability of capelin and the incumbent climate regime. Such conclusion is supported by the overwhelming presence of adult cod (age-3 and older) during fall-winter months (prior to their spawning migration) in the areas where we detected the low age-0 cod survival (cf. Figs. 2 and 5). This is particularly applicable to cod larger than 50 cm. However, during the months that separate the summer-fall and the winter survey, the geographical incidence of age-0 and age-1 cod in the stomach of older than age 3 cod is high only in the shallow areas of the critical region for age-0 cod survival (cf. Figs. 2 and 6). It is therefore possible that the low age-0 cod survival detected in the deep portion of the central critical area is actually due to active migration of pre-settling cod toward shallow areas. Once in shallower areas age-0 cod (becoming age-1) may then become more vulnerable to the predation from adult cod. Alternatively, it is possible that the incidence of young cod in the stomachs of adult cod caught in the deeper areas of the bottom trawl survey is actually underestimated, being the proportion of adult and young cod that reside in the water column greater in deeper areas (Hjellvik et al. 2002).

Future directions that we intend to pursue in our study are to device a better annual index of age-0 cod spatial survival, an index that can better account for the density of age-0 cod in the areas which were not surveyed in the winter. Also, we intend to examine the effect of other covariates on the variability of age-0 cod spatial survival. These include zooplankton biomass, bottom water temperature in winter and age-0 ambient temperature in summer-fall, and to address density-dependent effect of spatial survival, also the density of the age-0 stage. While the spatial distribution of cod eggs and larvae during the pelagic phase mainly is 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 (see, e.g., Swain and Wade, 1993) may, to a certain degree, affect the spatial distribution and the survival at later stages. The effect of an increase in distribution range on the survival of age-0 cod are yet unresolved and are likely to depend on the state of the other examined environmental covariate (e.g., water temperature, climate, capelin and adult cod abundance).

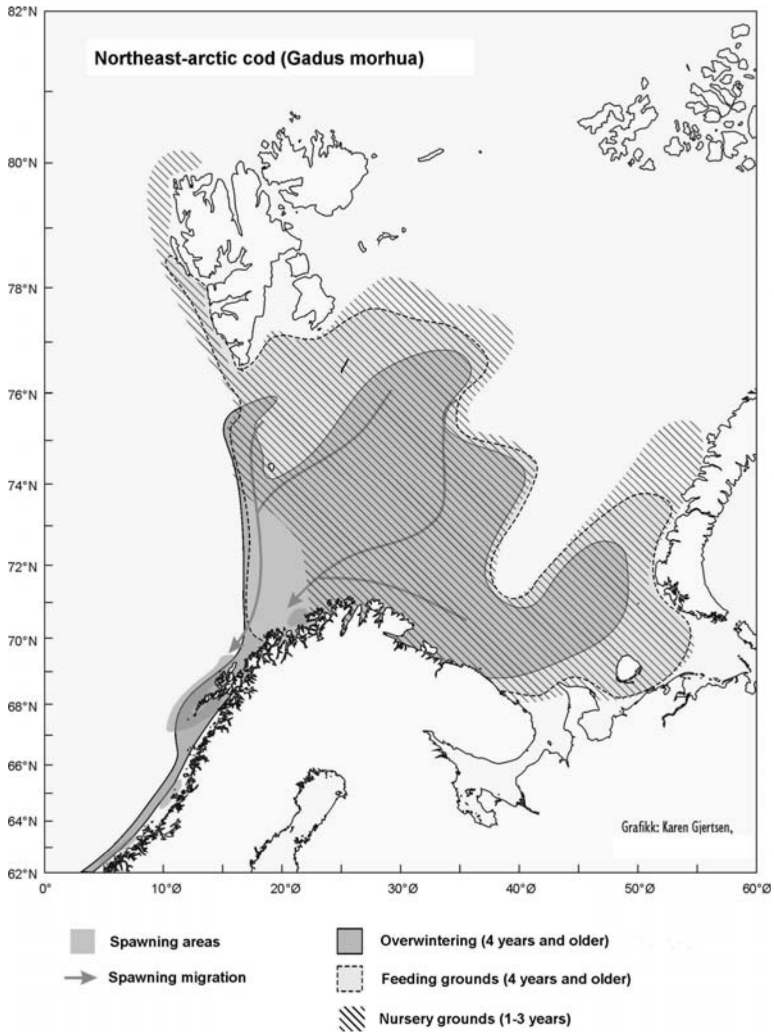

Figure 1. Spawning, overwintering, feeding and nursery areas for the Arcto-Norwegian cod. The arrows indicate spawning migration patterns.

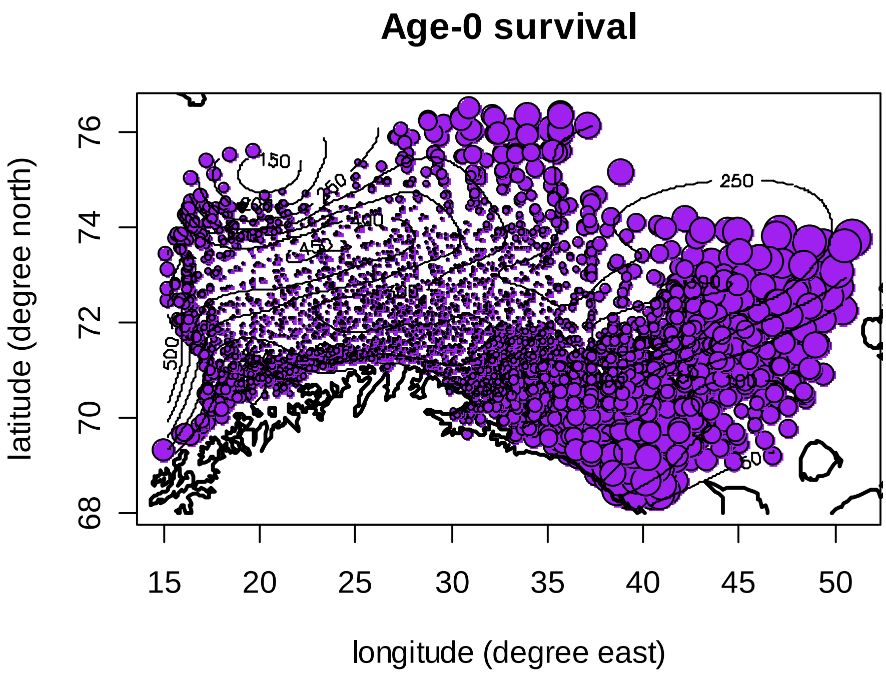

Figure 2. Average spatial patterns of age-0 cod survival from 1980 to 2004 as determined from a GAM model including geographic coordinates (latitude and longitude) and bottom depth as covariate. Circles are proportional to the geographic effect. Also shown is the depth contour (black lines).

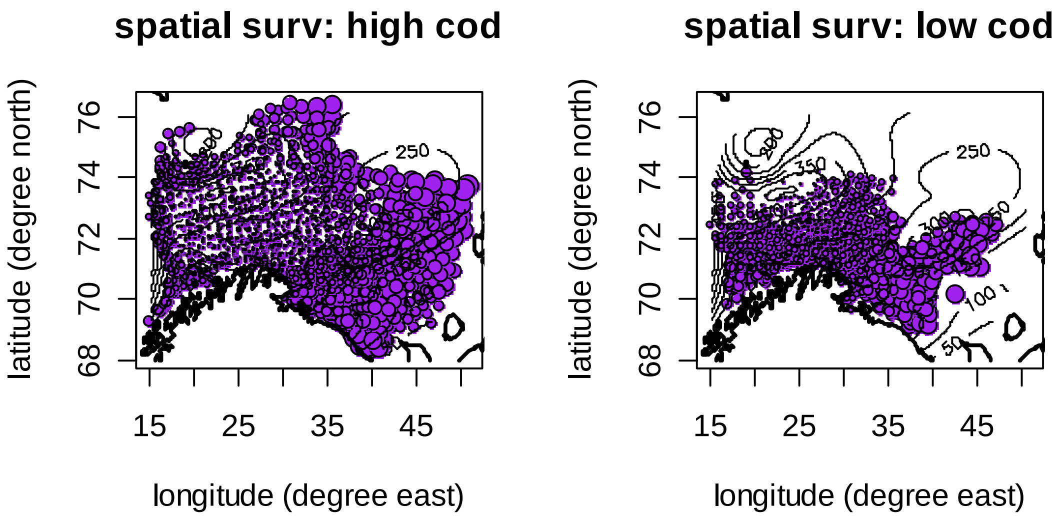

Figure 3. Spatial pattern of age-0 cod survival during years with high (left) and low (right) cod biomass.

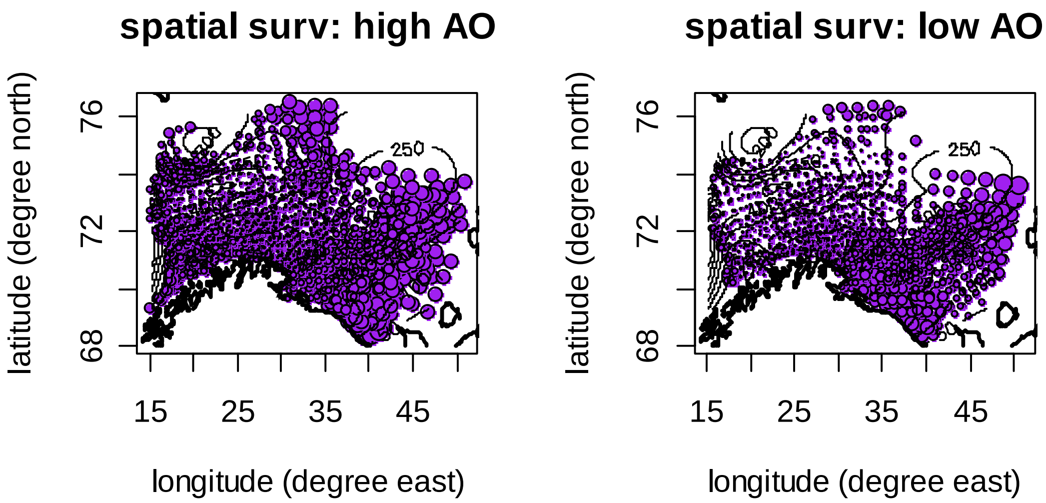

Figure 4. Spatial pattern of age-0 cod survival during years with high (left) and low (right) AO index.

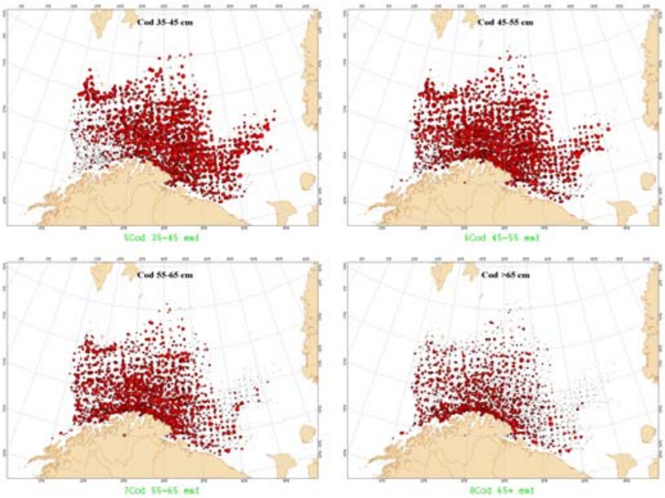

Figure 5. Average distribution of adult cod (1981-2005) during the winter survey, partitioned by size categories.

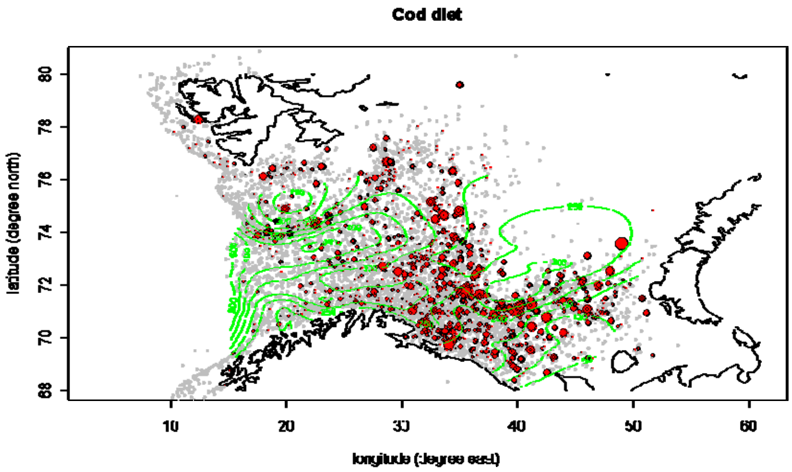

Figure 6. Geographic distribution of cannibalism by adult cod on age-0 and age-1 juvenile cod, during the months separating the summer-fall from the winter survey. Circles are proportional to the partial fullness index (PFI), a gravimetric measure of stomach content standardized by predator length (Dalpadado and Bogstad 2004).

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