Landscape dynamics and predator-prey interactions in marine environments

L. Ciannelli, K. Bailey, K. Frank, D. Hjermann, G. Ottersen, N.C. Stenseth.

Lorenzo Ciannelli: Centre for Ecological and Evolutionary Synthesis, University of Oslo, Department of Biology. PO Box 1050 Blindern N-0316 Oslo, Norway [tel: +1 47-22 85 50 65, fax +1 47-22 85 46 05, email: Lorenzo.Ciannelli@noaa.gov. Kevin Bailey: Alaska Fisheries Science Center, NOAA, 7600 Sand Point way NE, Seattle WA, 98115 [tel: +1 206-5264243 fax: +1 206-5266723, email: Kevin.Bailey@noaa.gov]. Kenneth Frank: Department of Fisheries and Oceans, Bedford Institute of Oceanography, Ocean Sciences Division, 1 Challenger Drive, Dartmouth, Nova Scotia, B2Y 4A2, Canada [Phone: (902)426-3498; Fax: 426-6927; email: FrankK@mar.dfo-mpo.gc.ca]. Dag Ø. Hjermann: Centre for Ecological and Evolutionary Synthesis, University of Oslo, Department of Biology. PO Box 1050 Blindern N-0316 Oslo, Norway [tel: +1 47-22 85 47 95, fax +1 47-22 85 46 05, email: d.o.hjermann@bio.uio.no. Geir Ottersen: Institute of Marine Research, Post Office Box 1870 Nordnes, N-5024 Bergen, Norway. Current address: *Centre for Ecological and Evolutionary Synthesis, University of Oslo, Department of Biology. PO Box 1050 Blindern N-0316 Oslo, Norway [fax +1 47-22 85 46 05, email: geir.ottersen@bio.uio.no]. Nils Chr. Stenseth: Centre for Ecological and Evolutionary Synthesis, University of Oslo, Department of Biology. PO Box 1050 Blindern N-0316 Oslo, Norway [fax +1 47-22 85 46 05, email: n.c.stenseth@bio.uio.no]*

Abstract

In several sub-arctic marine ecosystems of the North Atlantic capelin are the primary prey item for cod, and the trophic interaction between capelin and cod is a central energetic pathway. However, in the North Pacific capelin are, in spite of their high abundance, barely represented in the diet of cod. In the Bering Sea this uniquely weak trophic link is the consequence of oceanic landscape features (e.g., bathymetry, hydrography, currents, and presence of suitable spawning areas) that generate a barrier between the centers of distribution of cod and capelin. Climate forcing influences labile features of this distributional barrier (i.e., hydrography) and may result in greater/lower predator-prey overlap through the opening of thermal gateways and corridors. In the current study we compare the results from the Bering Sea with those from the Barents Sea, where cod are strongly dependent on capelin as prey. Through this comparative analysis we wish to illustrate the importance that oceanic landscape and climate forcing have on the spatial overlap and trophic interactions between predator and prey. Spatial considerations are seldom accounted for in population dynamics models, even though the mechanisms that promote overlap variability can indirectly have profound effects on population demographic rates. In that regard we believe that our analysis is relevant to better comprehend the mechanisms leading to regime shift of marine forage population dynamics in the presence of climate forcing.

Introduction

In many of the world's northern seas, the distributions of cod (*Gadus* spp.) and capelin (*Mallotus villosus*) overlap (Lilly 1994, Rose & O'Driscoll 2002), and their predator-prey relationship is a trophic interaction of high relevance for the entire ecosystem (e.g., Dolgov 2002). In the Barents Sea, for example, Atlantic cod (*Gadus morhua*) feed on capelin year-round. The importance of capelin in the cod diet varies from year to year, and the percentage of total biomass consumed may be greater than 50% (Nakken 1994), mainly depending on the availability of capelin as prey (Dolgov 2002). Capelin are also a critical component of cod diet in other areas where their distributions overlap, including the northwest Atlantic (Lilly 1991, 1994) where capelin makes up about 10-40% of the diet of cod and in the seas around Iceland where capelin makes up 25-90% of the cod diet (Palsson 1997). Moreover, it has been observed that the reproductive potential and the liver index of cod are closely linked with the abundance of capelin. For the northern cod stock from the Newfoundland area and Labrador Sea, this implies that a rebuilding of the cod stock in this region may be dependent to a return of capelin (Rose & O'Driscoll 2002).

In contrast to the North Atlantic ecosystems, the capelin in the eastern Bering Sea play a relatively insignificant role in the diet of the Pacific cod (*Gadus macrocephalus*). Generally, capelin makes up about 1% of the diet of cod in Bering Sea (Livingston and deReynier 1996). While relatively little is known about the overall capelin abundance in the Bering Sea, they have been historically identified as a key linkage in the food chain. Capelin are in fact an important component of the diet for many seabirds (Springer et al. 1987), seals (Lowry and Frost 1981) and whales (Frost and Lowry 1981). Furthermore, declines of capelin stocks have been proposed as a potential cause of a declining Pacific fur seal population in the Bering Sea (Sinclair et al. 1994).

In this study we examine the link between landscape dynamics, climate forcing and ecological interactions between cod and capelin across two contrasting ecosystems: the Bering Sea and the Barents Sea. We argue that the oceanic landscape features regulate the overlap between the predator (cod) and the prey (capelin) largely determining their trophic interactions. We furthermore hypothesize that climate forcing can influence the ecological interactions between cod and capelin by modifying the landscape constraint to their distributions. In general, through the present study, we wish to highlight the importance of landscape ecology and its dynamics on oceanic species interactions, an outlook that may enhance our understanding of predator-prey interactions in a temporally and spatially dynamics environment.

Background and methods

Bering Sea

The continental shelf of the Bering Sea is broader than 500 km. It is divided into three distinct pelagic zones: the outer, middle and inner shelves. These domains are separated by two frontal regions at the 50 and 100 m isobaths that are created by tidal interactions with topography; the outer shelf lies seaward of the 100 m front, the middle shelf zone is between the 50 and 100 m fronts, and the inner shelf is inland of the 50 m front (Stabeno et al. 1999; Fig. 1A).

We examined distribution patterns of cod and capelin in relation to bathymetry, and hydrography. Data on cod and capelin distribution (i.e., catch at location) in the

Bering Sea were taken from the bottom trawl survey of the Alaska Fisheries Science Center (AFSC; Nebenzahl 2001). Sampling occurred during the summer months, typically from the end of May to the end of July and data are available on an annual base since 1972. Catches were recorded as biomass over area swept (kg ha^{-1}), and will hereafter be referred to as catch per unit effort (CPUE). Along with CPUE, also bottom depth, and bottom and surface temperatures were recorded at each station.

Generalized Additive Model (GAM) analysis was used to investigate the factors affecting the incursion of cod in the inner portion of the Bering Sea shelf, where typically capelin were more densely aggregated. We assessed the spatial overlap between cod and capelin as the product between the distance-weighted cod and capelin CPUE, at the examined station (Ciannelli and Bailey MS). Finally we used linear regression analysis to inspect the correlations between a North Pacific climate index (i.e., Pacific Decadal Oscillation index, PDO) with the annual overlap index between cod and capelin and with the width of 1-6°C thermal gateway across the middle shelf (Ciannelli and Bailey MS).

Barents Sea

The BS is an open arcto-boreal shelf-sea with an average depth of 230 m, covering an area of about 1.4 million km^2 (Fig. 1B). Although located from around 70ºN to nearly 80ºN, sea temperatures are substantially higher than in other regions at similar latitudes due to inflow of relatively warm Atlantic water masses from the southwest (Loeng 1991). There are three distinct water masses in the Barents Sea: the Atlantic, the Arctic and the coastal waters (Fig. 1). The Atlantic water, in the southwest, is warm (> 3°C) and has high salinity (> 35°/$_{oo}$). Sea temperatures in the Atlantic water masses of the Barents Sea seldom go below 3-5 ^{o}C in winter and 5-10 ^{o}C in summer (Johannessen 1986, Loeng 1991). The Arctic water, in the north, is characterized by salinities of 34.3-34.8 and temperatures typically lower than 0°C. Finally, the coastal water in the proximity of northern Norway and Russia, has temperature similar to the Atlantic water, but much lower salinity, < 34.7 (Sakshaug et al. 1994). The Barents Sea is divided into two domains by an oceanographic Polar Front, separating the Atlantic and Arctic water masses. The Polar front is distinct and locked to bathymetry at 75-76 ^{o}N in the west, while it is more diffuse and spatially varying in the east. The western part of the region south of the Polar Front is permanently ice free (Sakshaug 1997).

The location of the Polar Front influences a number of biological processes of the Barents Sea, including primary and secondary production (Sakshaug, 1997). Furthermore, the distribution of pelagic (e.g., capelin) and demersal (e.g., cod) resources are linked to interannual variability in temperature conditions (Gjøsæter 1998, Nakken and Raknes 1987, Ottersen et al. 1998). The review of cod and capelin distribution in relation to thermal conditions of the Barents Sea, that we present in this study, is based on a synthesis of published papers.

Results

Bering Sea

The distribution of cod and capelin in the Bering Sea is strongly linked with bathymetry and bottom temperatures. Summer bottom temperature of the Bering Sea have a unique spatial pattern, characterized by the extension, over the middle shelf, of a cold pool (0-3°C; Fig. 2).Warmer bottom temperatures are typically found in coastal

zones and in the outer shelf. Such pattern is strongly influenced by physical features, such as bathymetry, ice cover, tidal and wind mixing. Specifically, warming of the bottom temperature near the coastal zone and offshore reflect tidal mixing of warmer surface water and advection of warm basin water onto the outer shelf, respectively. Cooling in the northern and central areas reflect the formation of the cold water mass, due to ice cover over the middle shelf in winter.

From their mean distribution patterns, cod are found in three main aggregations in summer: one on the western side of the outer shelf in water 100-200 m deep, the second in the middle shelf northeast of the Pribilof Islands in water that is 50-70 m deep, and the third along the Alaska Peninsula (Fig. 3). In summer capelin are distributed in the northern coastal region, typically in water shallower than 70 m (Fig. 3). In years when a frigid water mass is over the middle shelf (i.e., $<2^{o}C$), there is a tendency for cod to be constrained to the outer region of the shelf, and to reside within a very narrow strip along the Alaska Peninsula. Conversely, when large thermal gateways (i.e., areas between the outer and the inner shelf with temperatures $> 2^{o}C$) penetrate the middle shelf, cod move to the north, and more densely and widely reside along the Alaska Peninsula (Fig 4). Capelin have an even clearer relationship with variation of thermal conditions over the middle shelf: in cold years, they move south and into Bristol Bay, while in warm years capelin move to the north and probably extend out of the surveyed region (Fig. 4).

The GAM analysis revealed that cod incursions from the outer to the middle and inner shelf of the Bering Sea were correlated with the average cod CPUE in the full survey area and with a linear interaction between cod CPUE and PDO index. The interaction term caused the cod CPUE in the middle and inner shelf region to roughly duplicate its value going from years with lowest (e.g., 1975, 1999) to highest PDO index (e.g., 1987, 1983). Such GAM regression model explained 84.7% of the total interannual variance of cod CPUE in the middle and inner shelf. In turn, the PDO index was weakly correlated with the width of thermal gateways in the inner shelf ($P = 0.034$, $r = 0.39$) and more strongly correlated with the overlap index between cod and capelin ($P = 0.026$, $r = 0.40$).

Barents Sea

Annual mean temperatures in the areas inhabited by Arcto-norwegian cod range from 6-8 ^{o}C at the most southerly spawning grounds on the west coast of Norway (Aure & Østensen 1993) down to subzero along the polar front in the summer and autumn feeding areas in the northern and north-eastern Barents Sea (Mehl et al. 1985). Spatial variations of cod distribution are observed in relation to age-classes; typically there is a tendency for younger age classes to reside in eastern and colder region of the Barents Sea (Fig. 6; Ottersen et al. 1998). During winter adult cod (age 6+) move southward to the spawning grounds of the Lofoten Islands, while the immature cod moves towards the western/southern part of the Barents Sea (in part following the mature capelin towards their coastal spawning grounds). In general, the distribution of cod within the Barents Sea is typically extended towards the cold eastern and northern parts in warmer periods compared to colder periods when the fish tend to concentrate in the south-western region (Nakken and Raknes 1987, Ottersen et al. 1998). However, this may not always be the case. In 1994, which was significantly colder than 1990, the cod were distributed over a larger area and further north and east (Fig. 7). This could reflect a time lag in the response of cod to a change in climate conditions. The northward and eastward extensions of the 1994

cod distribution may in fact reflect a response to the warm conditions that prevailed in the early 1990s (Ottersen et al. 1998).

The BS stock of capelin is the largest in the world, with a biomass that in some years reaches 6-8 million metric tones. Capelin plays a key role as an intermediary of energy conversion from zooplankton production to higher trophic levels, annually producing more biomass than the weight of the standing stock (Gjøsæter 1998). The capelin undertake extensive seasonal migrations. During winter and early spring they migrate southwestwards to spawn along the coast of northwest Russia and northern Norway. In summer and autumn they migrate back north- and northeastwards to feed along the ice edge (Gjøsæter 1998; Fig. 8). At this time, capelin is in general distributed further east and north than cod. However, the two species overlap in the areas close to Bear Island and Spitzbergen (Dolgov 2002). Both spawning and feeding areas of the capelin varies extensively with sea temperature. Typically, during warm years the center of feeding and spawning distribution is shifted eastward (and northward in the case of feeding) compared to cold years (Tjelmeland 1987, Loeng 1989, Gjøsæter 1998, Orlova et al. 2002; Fig. 9). Cod feed on capelin mainly in two periods of the year: first, during the capelin's spawning migration in February and during the spawning itself by the Norwegian coast in March and April, and second, in August-September where the capelin's feeding grounds overlap with the cod's distribution.

Discussion
Bering Sea dynamics
      The migration pathways of cod and capelin, as determined by the ocean landscape, in large part regulate the overlap of predators and prey in the studied systems. In the southeastern Bering Sea, capelin are mainly distributed in the near coastal region, in water shallower than 70m. In part, capelin movements are also tied to the location of suitable spawning habitat, sand and cobble beaches, which are distributed all along the shore-side of the eastern Bering Sea. Although little is known about capelin seasonal movements, it appears that after spawning, in summer, a part of the population may migrate northwards towards feeding grounds in the northern sea. Cod do not appear to have a consistent interannual distribution range, indicating that their movements may be linked to more than one of the variable hydrographic features of the Bering Sea shelf. However, their center of distribution is consistently located further south than that of capelin.

      The dynamics of the landscape and species interactions likely have important consequences to the dynamics of both cod and capelin in the Bering Sea. The interactions between cod and capelin are confined to the middle and the inner portion of the shelf and are linked with the formation of corridors and critical habitat junctions between the outer and inner/middle shelf regions. Climate may regulate the extent of cod migration and overlap with capelin, via a regulation of the thermal regime and gateways width in the middle shelf of the Bering Sea. In our analysis, the PDO index was correlated with the degree of overlap between cod and capelin, with the relative abundance of cod in the inner shelf and with the width of the thermal gateway, suggesting a direct causal link going from climate and thermal gateways to predator-prey overlap. However, other factors were also important in regulating the incursion of cod in the north capelin territory. For example, the non-linear effect (i.e., slightly convex) of cod CPUE from the

full surveyed region on that found further north, is indicative of a positive density-dependent movement from the outer shelf to the middle and inner shelf (a density-independent effect would result in a linear term). Thus, the inner and middle portion of the shelf may be an overflow region for cod, occupied when thermal conditions are favorable (i.e., wide gateway) and when stock abundance is high. Indeed, this hypothesis is supported by the significant interaction between PDO and cod CPUE of the GAM analysis. A wider dispersion at higher population size has also been found in several flatfish stocks of the Bering Sea (McConnaughey 1995), as well as for Atlantic cod (Swain and Wade 1993).

Barents Sea dynamics

In the Barents Sea the seasonal migration patterns of cod and capelin to a large degree determine their spatial overlap and trophic interactions. Seasonal variation of capelin in cod stomachs varies annually with a peak during February-April (> 40% of diet in weight; Dolgov 2002), when the pre-spawning capelin must pass through a gauntlet of immature cod. However, the impact of cod on the capelin stock may also be high in the summer, when cod feeding requirements are typically higher and when the entire cod stock (not only the immature portion) is feeding on capelin. Given the fixed geographical constraint imposed by the location of suitable spawning areas on capelin movement it is reasonable to assume that the degree of spatial and temporal overlap between cod and capelin during winter varies mostly in relation to the biomass of the two species, rather than to labile hydrographic features. In contrast, during summer months hydrographic features may play a more pivotal role in determining the overlap and the extent of trophic interactions. In this season, the distribution of capelin appears to be more heavily affected by climate than that of cod, which may be more linked to the shallow areas, such as the banks in the Bear Island/Spitzbergen area. From the distribution patterns we infer that in cold summers, a larger part of the capelin population feeds in these shallow areas, and is therefore more susceptible to cod predation.

Previous studies clearly show that the amount of capelin found in cod stomachs and the annual body growth of cod are dependent upon the available capelin biomass (e.g., Dolgov 2002, Hjermann et al. 2004a). In turn, capelin availability also affects the liver condition index of the Barents Sea cod (Yaragina and Marshall 2000) and ultimately their egg production and recruitment (Marshall et al. 1999). Hjermann et al (2004b) showed cod predation may delay the rebuild of capelin stock after collapse (e.g., 1986). Collectively these studies point to the importance of cod-capelin predator-prey interactions in their respective population dynamics.

Comparative remarks

There are a number of important differences in the landscape features of the Barents and Bering Sea that may explain the contrasting trophic interactions between cod and capelin in these two seas. A major difference appears to be in the constraint imposed on cod movements by the cold water pool over the middle shelf of the Bering Sea, whereas no such constraint forms in the Barents Sea. As a consequence, during summer capelin and cod are in close proximity in the Barents Sea, while they are separated by a thermal barrier in the Bering Sea. Another difference is in the suitability of capelin

spawning locations: in the Barents Sea capelin have to cross the cod stock to spawn, while in the eastern Bering Sea capelin spawns along northeastern shorelines, where cod is not abundant.

Landscape dynamics, as affected by climate forcing, may reverberate at the population level through a variation of predator-prey trophic interactions. In the Bering Sea for example, during warm environmental regimes the overlap between cod and capelin increases and may cause a trophic cascade. Examples include the disappearance of the capelin stock in the outer shelf in the late 1970s and the lack of a capelin return to the southern shelf in spite of a period of relatively cold thermal conditions (i.e., late 1980s). In the Barents Sea, cod-capelin interactions have clearly shown to affect the dynamics of both populations (e.g., Tjelmeland and Bogstad 1998, Marshall et al. 1999, Hamre 2003, Hjermann et al. 2004b). Previous attempts to model cod-capelin trophic interactions have mostly been done in relation of stock biomass (e.g., Hjermann et al. 2004b). Spatial components have been also considered, but only in relation to seasonal migration pathways, which were assumed invariant from one year to the next (Tjelmeland and Bogstad 1998). However, it seems highly likely that the inter-annual variability of spatial overlap between cod and capelin, resulting from changes in climate and labile landscape features (i.e, hydrography), also plays a central role in their population dynamics. We speculate that the link between landscape variability and cod and capelin population dynamics is particularly important during summer months, when the distribution of capelin is more linked with water temperature, and when the feeding requirements of the cod stock are higher.

Constraints imposed by landscape features may also have an evolutionary effect on several life history traits of cod and capelin. In the Barents Sea, for example, capelin reproduce in winter months (February-March) while in the Bering Sea capelin reproduce in summer (June). This difference may in part be an evolutionary adaptation to reduce predatory impact: by reproducing in winter capelin reduce considerably their predation mortality due to the lower food requirements of cod during winter months and to the presence of only immature individual in the Barents Sea (mature cod migrate south toward the spawning grounds).

Our study points to the fact that marine landscape features influence the spatial overlap between cod and capelin, and regulate their trophic interactions. Climate may influence the degree of such interactions by acting on the landscape. Spatial considerations, linked with climate forcing, are seldom accounted for in population dynamics models, even though the mechanisms that promote overlap variability can indirectly have profound effects on population demographic rates. In that regard we believe that our study, focusing on the landscape dynamic of marine systems, is relevant to better comprehend the mechanisms of population variability in the presence of climate forcing.

Fig. 1A. Map of the eastern Bering Sea with location of the surveyed grid from 1979-2001. During the years 1972-1978 the sampled grid was variable.

A
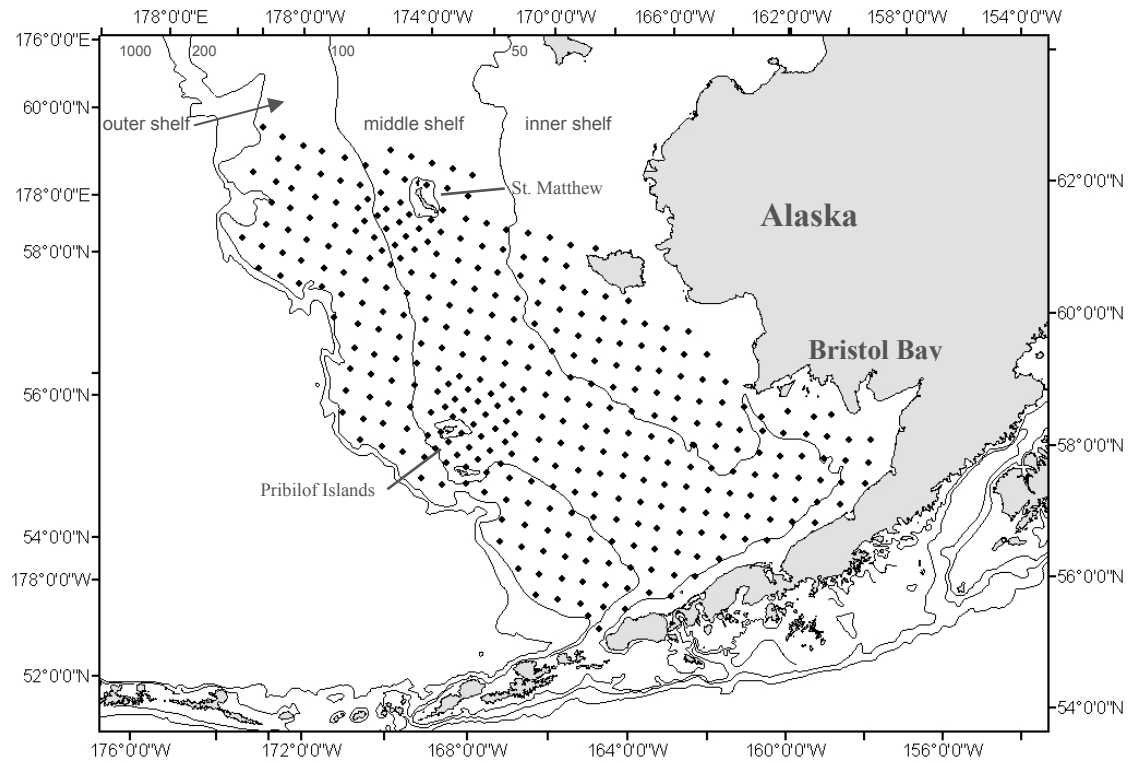
B. Map of the Barenst Sea, with bottom temperature contours and main water flows (blue = Arctic, red = Atlantic). Modified from: Fosså (2002).
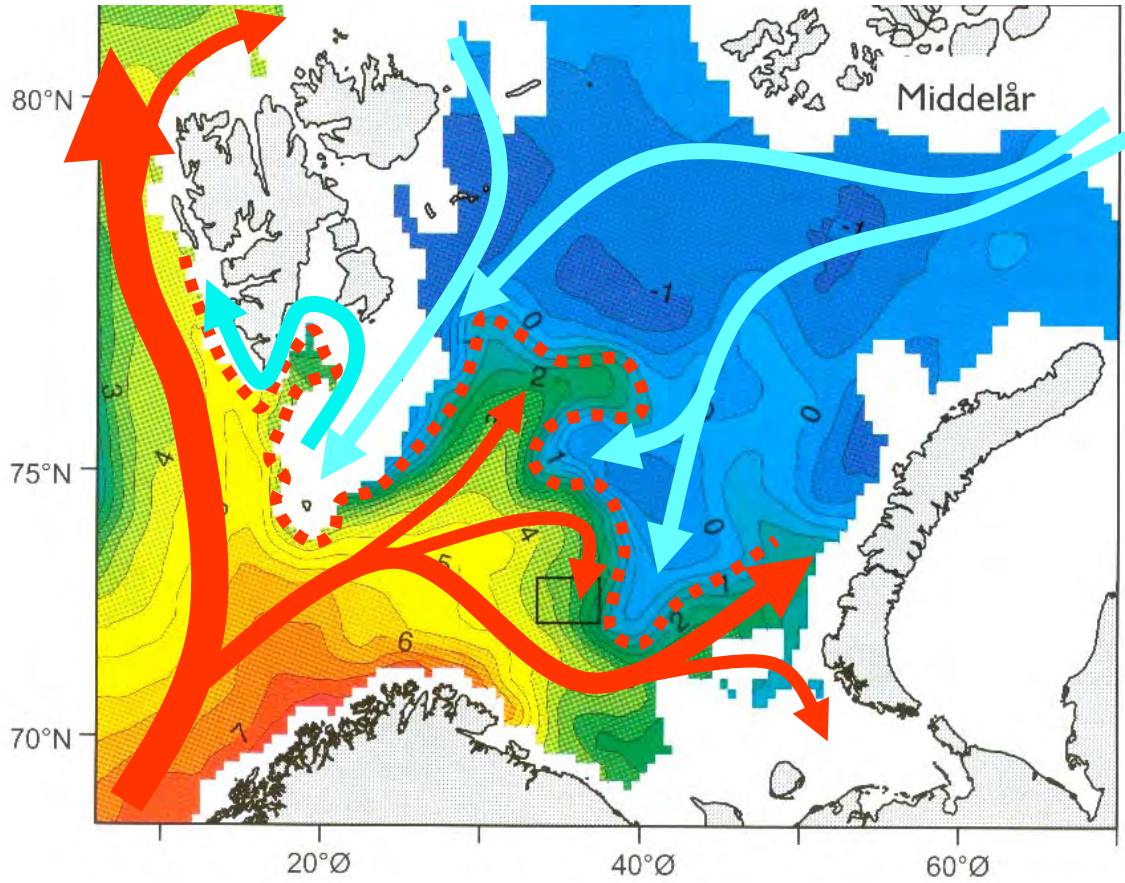
Figure. 2. Bottom water temperature in the eastern Bering Sea, average from1972-2001. Cool waters are located along the middle shelf (bottom depth between 50-100 m), forming a cold pool.
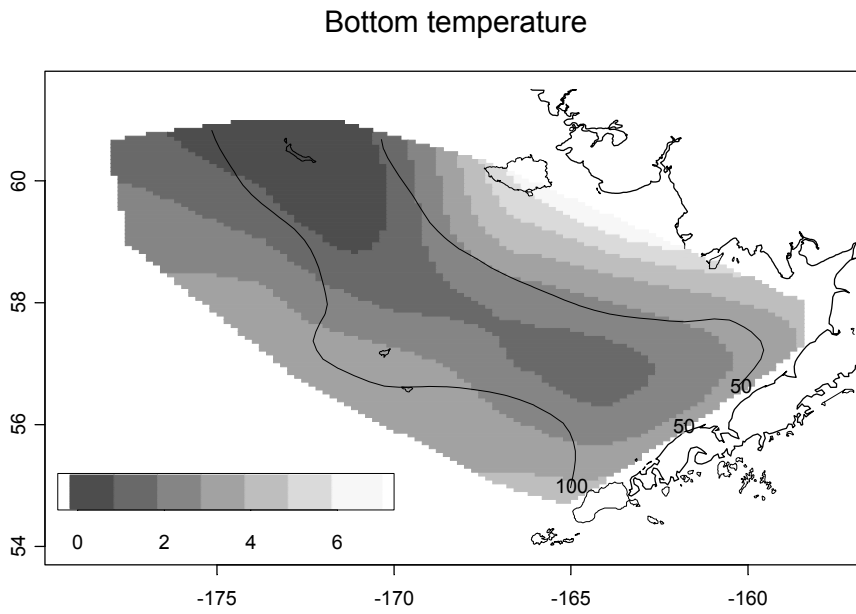
Bottom temperature

Figure 3. Cod (top panel) and capelin (bottom panel) average catch per unit effort (CPUE) in the eastern Bering Sea, average from 1972-2001.
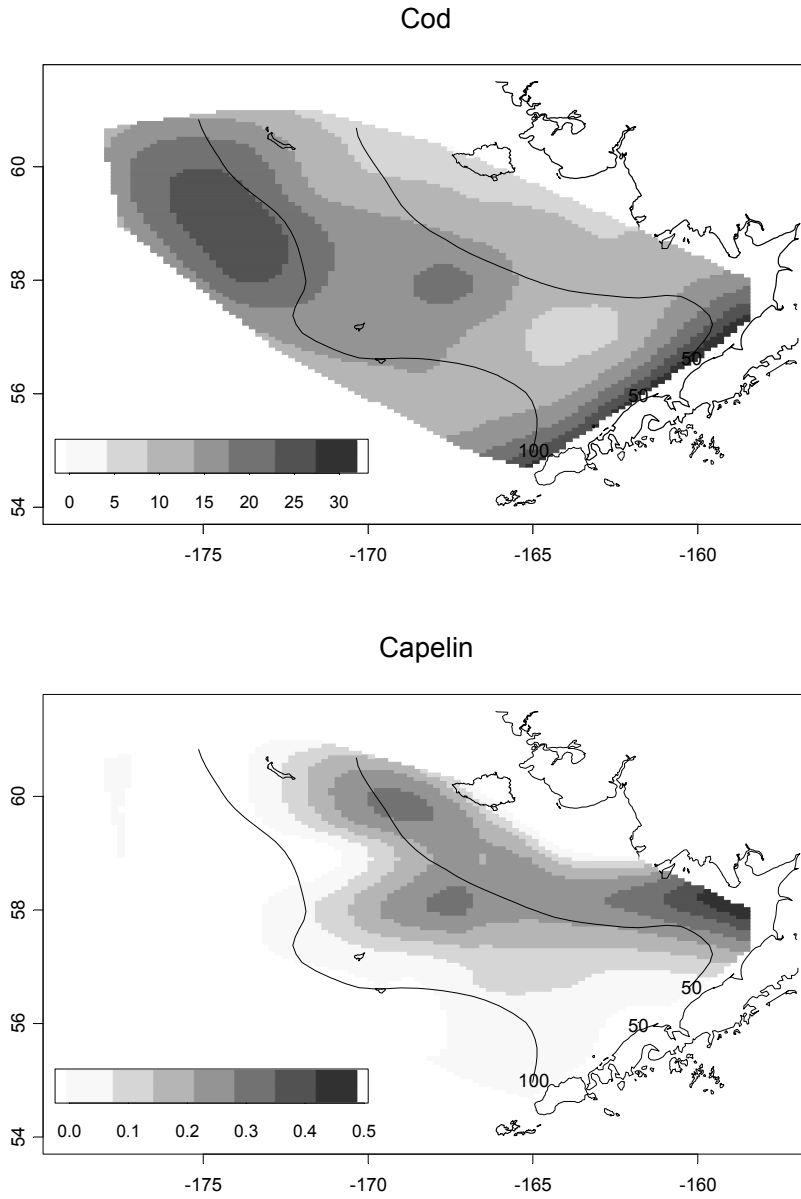
Figure 4. Cod (left panels) and capelin (right panels) distribution during years with narrow (top panels) and wide (bottom panels) thermal gateway in the middle shelf. Thermal gateways were defined as areas of the middle shelf with bottom temperature between 1-6°C.
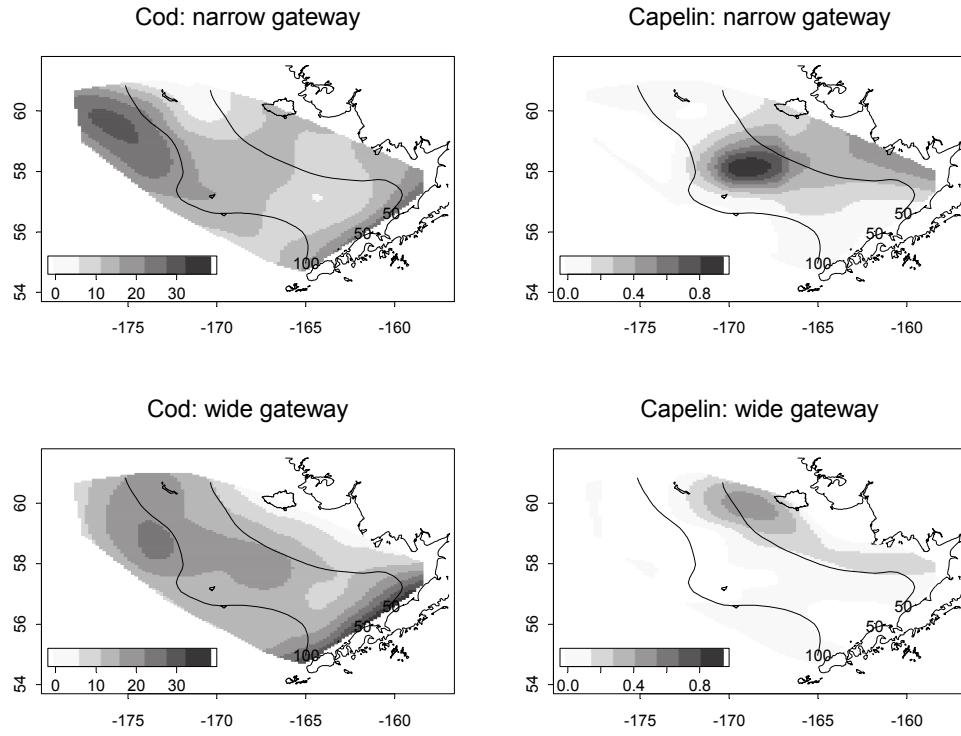
Figure 5. Predictions of cod CPUE in the inner/middle shelf of the Bering Sea (Cod North) as a function of cod CPUE throughout the survey area (total cod) and the Pacific Decadal Oscillation index (pdo). Predictions were derived from a generalized additive regression model (GAM) fitted to the 1972-2001 available time series. The model shown explains 84.7% of the interannual variability of cod CPUE in the inner/middle shelf.
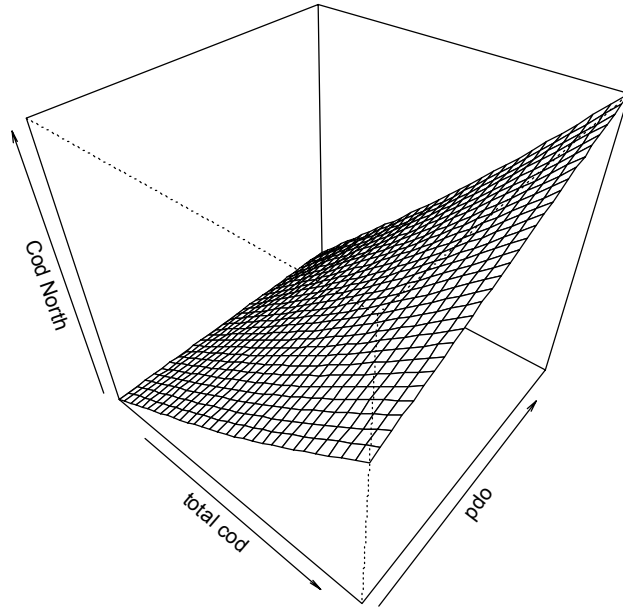
Figure 6. Cod distribution in winter for immature (6+; top) and mature (2 years old; bottom). From Mehl (1998).
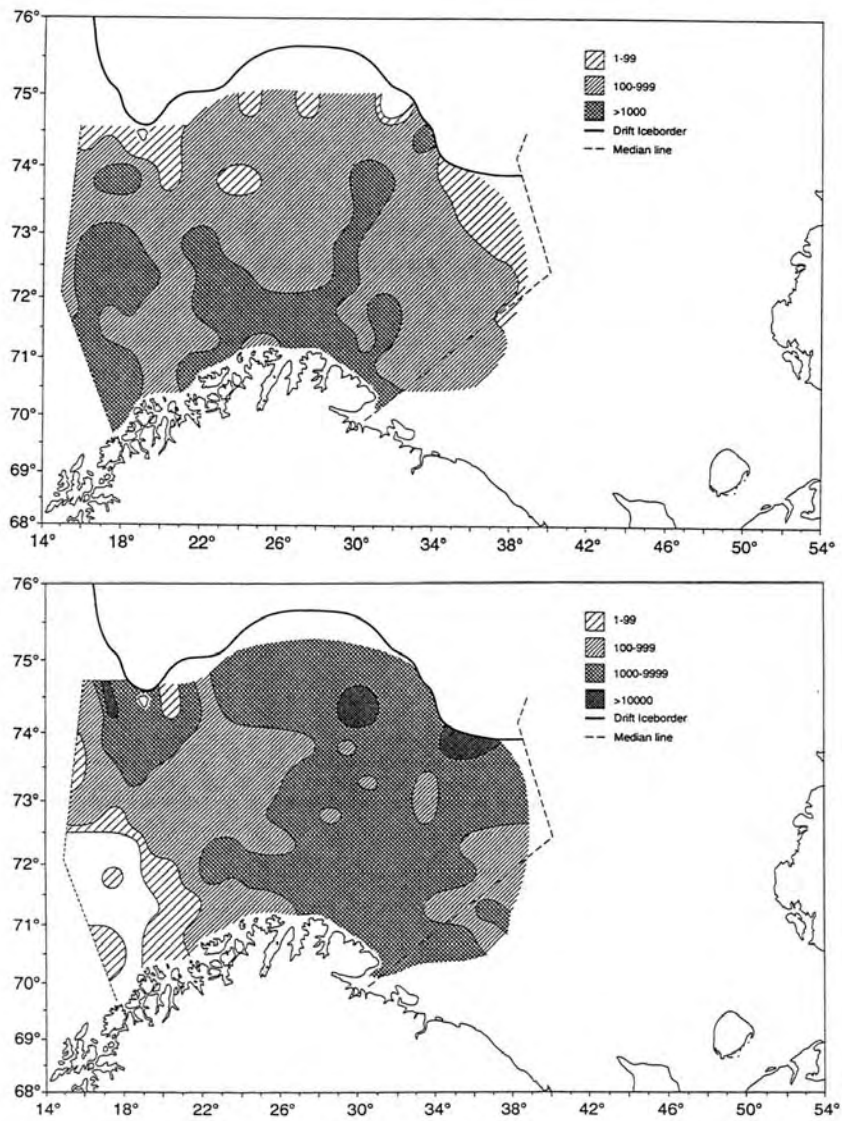
Figure 7. Distribution of bottom temperatures (isotherms, °C) and cod echo density (shaded areas) and in the Barents Sea during February 1990 (upper graph) and 1994 (lower graph). Back scattering coefficient, s_A of all cod. Darker shading indicates $s_A >$ 100 m^2/(nautical mile)^2. From Ottersen et al. (1998).
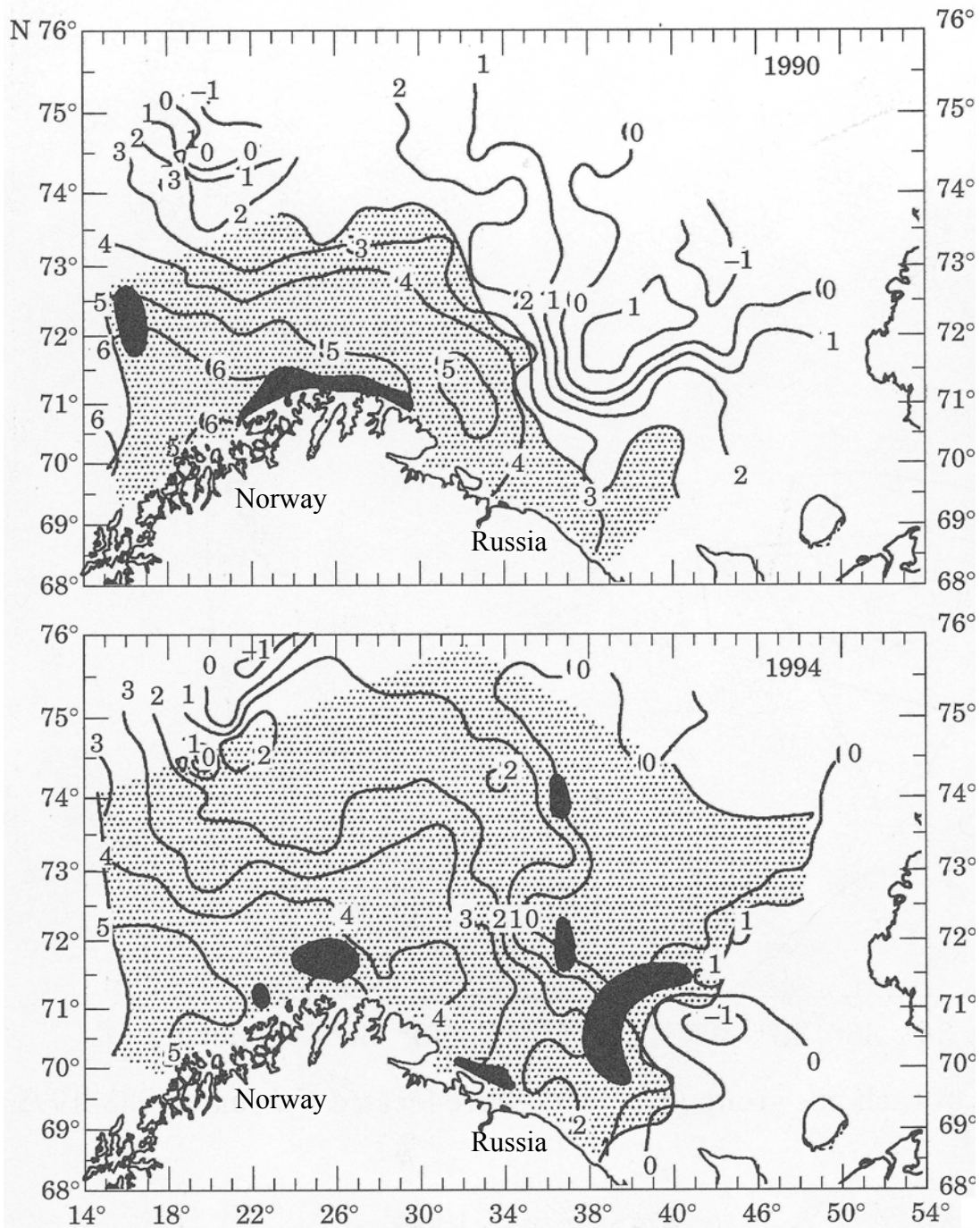
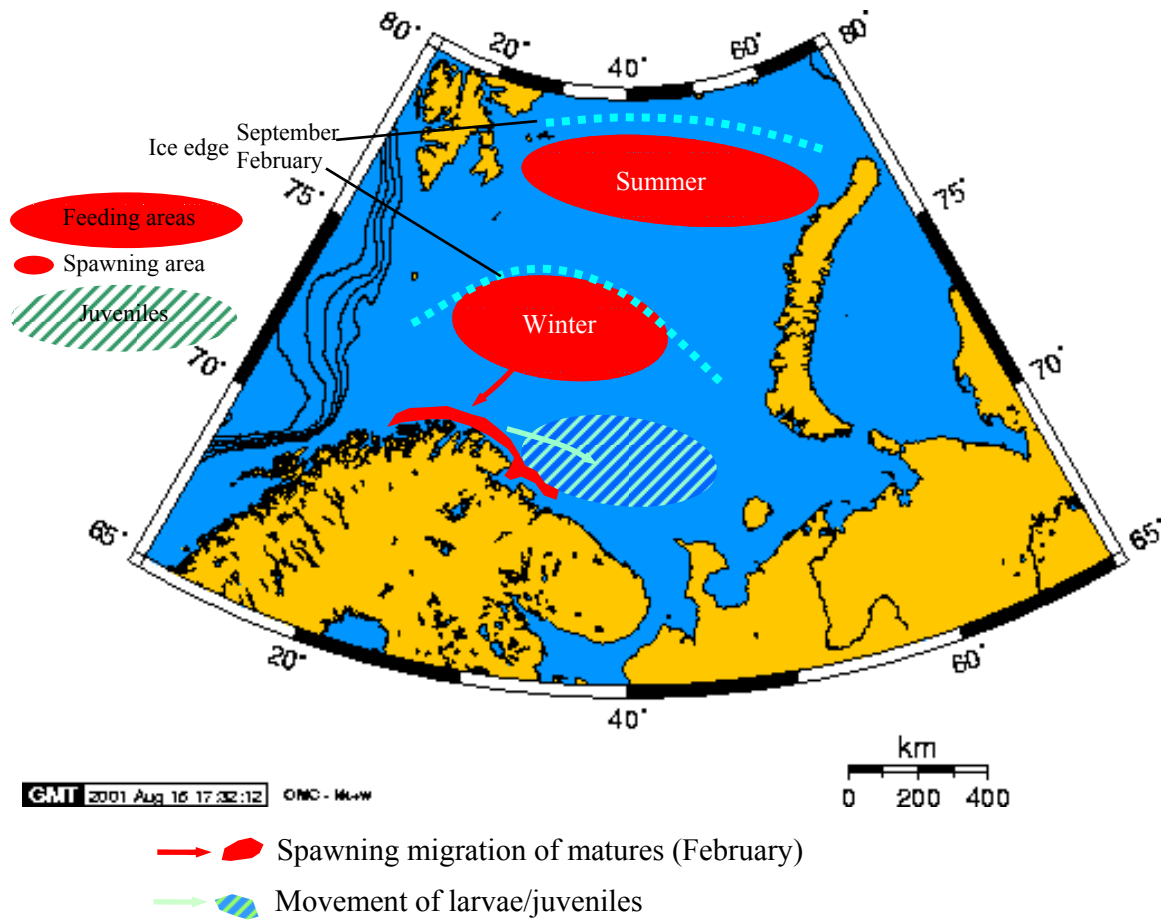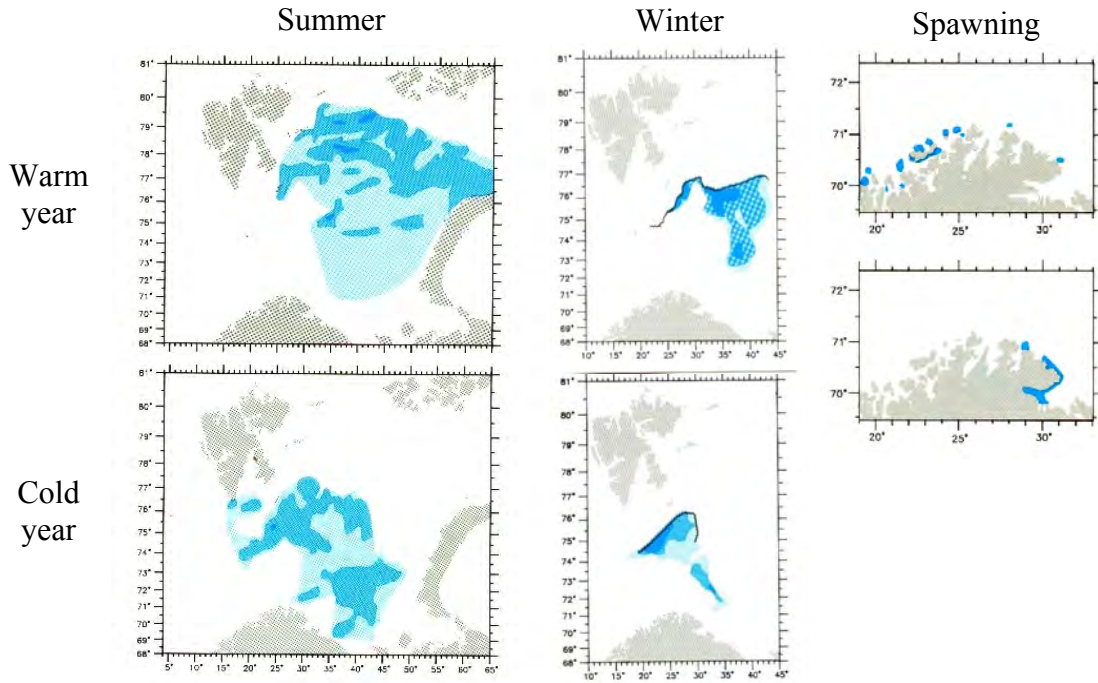Figure 8. Capelin seasonal distribution in the Barents Sea.

Figure 9. Summer and winter capelin distribution during warm (top) and cold (bottom) years. From Sakshaug et al. (1994).

	Summer	Winter	Spawning
Warm year			
Cold year			

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