



ORIGINAL ARTICLE

Responses in spatial distribution of Barents Sea capelin to changes in stock size, ocean temperature and ice cover

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Abstract

Using data for the period 1972–2010, we relate the variations in the Barents Sea capelin distribution to stock size, ocean temperatures and the area available for dispersal during summer. We find a strong relation between distribution area and stock size, which is most likely caused by a large stock extending the feeding area to meet the higher food demand. However, during the last decade there has been a general expansion of the distribution area and a northward shift of the high-concentration areas, which we relate to the high temperatures and low ice cover observed in the northern Barents Sea during the period. The study shows that ocean temperature and ice cover set the large-scale terms for the capelin distribution, while the stock size determines how capelin uses the available area. Changes of 4 million tonnes in stock size or 1°C in temperature give comparable impacts on the distribution.

Key words: *Barents Sea, capelin, ocean temperature, ice cover, ambient temperature, spatial distribution*

Introduction

The capelin *Mallotus villosus* (Müller, 1776) is the largest pelagic fish stock in the Barents Sea (BS) and is considered a key species in the ecosystem (Gjøsæter 1998 and references therein). The spatial distribution of the stock shows great variations (Gjøsæter 1998), which in turn impact the overlap between the capelin and its main prey and predators (Gjøsæter 1998 and references therein; Huse et al. 2004). Thus, understanding the factors influencing the variations in the capelin distribution is important for the overall understanding of the BS ecosystem variability.

Earlier studies have shown that the BS capelin distribution vary with the temperature conditions (Gjøsæter 1998 and references therein; Huse et al. 2004; Carscadden et al. 2013), and according to Rose (2005) the capelin react strongly and quickly to climate variability, thus making it a sea ‘canary’ for northern boreal marine ecosystem responses to climate variability and change. In accordance with this, a recent study has shown a northward shift of the Icelandic capelin associated with an observed ocean warming (Valdimarsson et al. 2012). Other studies, however, have found a weak relationship between the

capelin distribution and the BS temperatures, and concluded that density-dependent effects are more important than the marine climate (Fauchald et al. 2006). Hence a consistent understanding of how the capelin responds to changes in stock size and ocean temperature and ice cover is presently lacking.

Density-dependent effects are an important factor for the capelin distribution because the higher food demands that arise when the capelin stock increases may be met by expanding their feeding area (Gjøsæter 1999; Fauchald et al. 2006). Gjøsæter (1999) demonstrated a strong, negative correlation ($r = -0.61$, $P = 0.001$) between the ambient temperature (the average temperature in the depth interval 10–200 m weighted by the number of capelin) and the biomass of the capelin stock. The most probable mechanism was that when the stock is large, it needs to expand its feeding area, which implies that it has to spread out in the northern and eastern direction where temperatures are lower. Fauchald et al. (2006) also found that the distribution of one- and two-year old capelin was displaced when the abundance increased. Hassel et al. (1991) estimated that a capelin stock of 5 million tonnes would need to cover more

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than half the BS area to sustain its production, given that on average about 25% of the total zooplankton production was suitable as food for capelin. Thus, a varying stock size has a strong impact on the spatial distribution, and the biomass of this stock has changed considerably during the period (about 40 years) for which the stock size has been estimated (Gjøsæter 1998). Periods when the stock size has been above 3 million tonnes have alternated with periods when the stock almost collapsed. These collapses have been explained by changes in the ecosystem (Gjøsæter 1998), first and foremost by periodic inflow of herring juveniles to the area.

All fish have preferred temperature ranges, and temperature is considered the most pervasive environmental factor that limits the spatial distribution of marine fish (Christiansen et al. 1997). Additionally, temperature and ice cover variations often cause corresponding changes in the BS zooplankton production and distribution (e.g. Skjoldal et al. 1992; Orlova et al. 2010). Both effects can influence the capelin distribution, and several early investigations showed that the capelin migrated to the northeastern BS in warm years during the feeding season, while in cold years they resided in the central and southwestern regions (Gjøsæter 1998 and references therein; Huse et al. 2004). In this article we revisit this issue utilizing the longer time series available today.

The observed temperature variability in the BS is substantial and since the early 1970s there has been a long-term temperature increase in the southern parts of almost 1.5°C (Johannesen et al. 2012). All years 2004–2007 had higher annual mean ocean temperatures than during the last maximum (in 1938), and 2006 was the warmest year ever observed (Bogstad et al. 2013). The ice edge in late winter has been retreating northwards since the 1850s, but the retreat has been particularly strong since the 1960s and 1970s (Vinje 2001; Zhang et al. 2008). This makes the period 1972–2010 highly relevant for investigating ocean temperature- and ice-induced variability in the capelin distribution.

In this study we will focus on describing the variability in the spatial distribution of capelin near the end of the feeding season and how the distribution is affected by ocean temperature and ice. We assume that stock size and ocean temperature/ice affect the distribution independently, and therefore we attempt to analyse these two effects separately.

Background information

The BS is a high-latitude, shallow (mean depth 230 m) shelf area covering about 1,600,000 km² (Jakobsson et al. 2004). Warm and salty Atlantic Water is brought into the area by the Norwegian

Atlantic Current, and this water mass extends over the western and central parts of the BS (Figure 1). Smaller branches of subducted Atlantic Water also enter through the deeper trenches of the BS from the north and northeast (Figure 1). However, the northern parts of the sea are dominated by cold and less-saline Arctic Water. The borderline between the two main water masses is called the Polar Front, and the temperature gradient is fairly sharp in the western parts of the BS.

The BS is seasonally ice-covered. During winter the ice edge usually follows the oceanic fronts, and there is a strong relation between the ocean temperature and the winter ice extent (Vinje 2001). During spring and summer the ice edge retreats east- and northwards due to increased insolation and the relation to ocean temperatures is weaker. The ice edge is usually at its northernmost position in September. The variation in the position of the summer ice edge is substantial; some years the northwestern areas are ice-covered south to 77°N while other years the entire BS is ice-free (Figure 1).

The capelin (*Mallotus villosus*) is a small, pelagic, schooling fish in the smelt family with a circumpolar distribution in the Northern Hemisphere. There are stocks on both sides of the northern Pacific and in the Atlantic. Capelin is found in the Canadian Arctic, in the Newfoundland–Labrador area, around Greenland and Iceland. The largest capelin stock is found in the BS.

The BS capelin stock undertakes substantial seasonal migrations. From a central position in the BS in June, capelin make a feeding migration following the receding ice-edge north- and northeastwards utilizing the plankton bloom generated by the stabilizing effect of the melting process (Gjøsæter 1998 and references therein). The stock is most widespread in late summer and autumn, when it is found both north and south of the Polar Front.

Material and methods

Material

The data are based on observations made during annual scientific cruises to the BS in late August–early October (mainly September), 1972–2010. The geographical distribution and biomass of the total capelin stock were estimated from synoptic bioacoustic measurements (Gjøsæter et al. 1998). Hydrographic data were sampled on the cruises using a CTD (Conductivity, Temperature, Depth probe) and water bottle samples at separate stations taken along the survey path. The number of station profiles varied annually between 128 and 1144, with a total of more than 16,000 profiles over the study period.

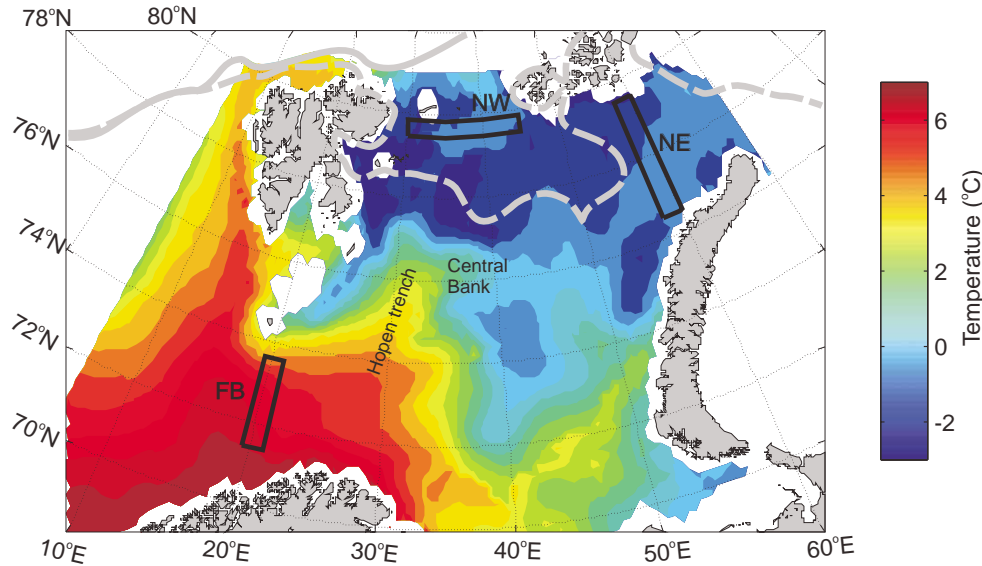


Figure 1. Mean temperature in August–early October for the 50–200 m depth layer during the period 1972–2010. The grey lines show mean ice edge (15% concentration) in September in the year with maximum ice cover (grey dotted line, 1982) and minimum ice cover (grey line, 2007). The black boxes show the location of the temperature series.

The Fugløy–Bear Island hydrographic section covers the Atlantic inflow region in the southwestern BS (Figure 1), and provides a good representation of the temperature variability in the southern region of the BS (Ingvaldsen et al. 2003). The section mean temperature from 71°30'N to 73°30'N in August–September, between 50 and 200 m, was used in the study.

The Summer Open Water Index (SOWI) is a quantitative, area-based measurement of the variation of the ice-free (ice concentration less than 40%) area north of 79°N integrated over the year. SOWI was calculated based on satellite derived sea ice maps available from the Norwegian Meteorological Institute (<http://met.no>). It was calculated for the segment between 25 and 45°E using $SOWI = \int_{\text{year}} (dY - 79) dt$ where dY is the latitude of the ice edge when $dY \geq 79$.

A high SOWI corresponds to a large fraction of open water while an index equal to zero means that the ice edge is south of 79°N throughout the summer season. During the feeding season the capelin are never observed close to the ice edge except in periods when the ice edge moved quickly because of strong winds. Therefore, the capelin is considered not to stay under the ice and hence the ice-free area denotes the area available for dispersal. Moreover, because the BS always is ice-covered north of 79°N in winter, this index is an indicator of the area experiencing seasonal ice melt and the associated plankton bloom. The index was compared to the more accessible ice area series from the National Snow and Ice Data Centre (NSIDC), and the two series were highly correlated. SOWI was preferred for this article as the series from NSIDC missed the first seven years of the study period.

Methods

Both the acoustic capelin data and temperature data at 0, 50, 100 and 200 m depths (from the hydrographic stations) were interpolated into a horizontal grid with a $\frac{1}{6}^\circ$ meridional resolution (18 km) and a $\frac{1}{2}^\circ$ zonal resolution (10–14 km). No extrapolation or smoothing was performed to the data, except for the implicit effect of the interpolation.

The centre of mass of the capelin distribution (CMD) was calculated as the mean (arithmetic) position weighted by the acoustic estimate. To compare and quantify movements of the CMD in the zonal (CMD_x) and meridional (CMD_y) directions, these are presented as distance (in km) from a fixed point (72°N, 20°E) and increasing eastwards and northwards, respectively. In addition to CMD, the distribution area (square km) of the capelin stock was calculated. In the 1970s, the surveys mainly covered the areas with high capelin abundance while the overall distribution area was not completely surveyed. Thus, in these early years the estimate of stock size and CMD are considered reliable, but the total area of the distribution is underestimated.

During autumn, the capelin undertakes vertical migrations. Due to the strong vertical gradients in temperature, particularly in the northern parts of the BS, and the fact that capelin tend to migrate vertically between cold, prey-rich areas during day time and warm waters at night (Huse et al. 2004), an average temperature of the water column seems most appropriate when studying capelin. Consequently, the gridded temperature data were combined into a mean 50–200 m field, and all temperatures and

water mass calculations are from the mean of the 50–200 m depth layer. To obtain temperature series from the northwestern and northeastern BS, the boxes (NW, 79°25′–79°50′N and 30–45°E; NE, 76°30′–79°30′N and 58–60°E, Figure 1) were defined and the mean temperatures were calculated in each box.

The ambient temperatures presented here are taken to be representative for the capelin during the growth season. The preferred temperature was calculated by binning the individual ambient temperatures into 0.5°C bins. Thereafter the temperature range covering at least 75% of the individuals was identified from the ambient temperature distribution by specifying that the cut-off of the tails on both sides of the distribution should be as equal as possible (~12.5% on each side). To ensure that this was actually a preferred temperature, the distribution was compared to the distribution of temperatures available for the fish.

In the years 2004–2007, capelin were also present west and north of Svalbard. This is outside their usual distribution area, but as this area only rarely was covered by the surveys in the earlier years, the historical presence of capelin in this region is largely unknown. Therefore, all analyses were performed exclusively on data east of 15°E and south of 80°N.

Numerical analysis

The relation between stock size and distribution area and CMD_Y was studied using linear methods. Due to the appearance of a strong linear correlation between capelin biomass and distribution area and CMD_Y , the effect of stock size on these variables was removed by linear regression. Thereafter the residuals from the regression analysis were compared to the abiotic time series. To account for possible shifts in relations over time, the comparisons were made using cumulative correlation coefficients. The cumulative correlation for year n is the correlation coefficient calculated from the start of the time series up to and including year n . The method of cumulative correlations was preferred to sliding window correlations because all years of the study period were included by this method.

To adjust for autocorrelation in the series, the effective number of degrees of freedom n^* was calculated for each cumulative correlation in accordance with Pyper & Peterman (1998): $\frac{1}{n^*} = \frac{1}{n} + \frac{2}{n} \sum_{j=1}^{n/5} r_{xx}(j)r_{yy}(j)$, where n is the sample size (up to and including year n), and $r_{xx}(j)$ and $r_{yy}(j)$ are the autocorrelations of the time series X and Y (up to and including year n), at lag j . A maximum of $n/5$ lags were included in the calculation of n^* (see equation above). The statistical

significance of the linear correlation coefficients was calculated using the derived effective number of degrees of freedom, and the significance criterion was 95% unless otherwise stated. All time series were normalized (means extracted and divided by the standard deviation) before the correlation analysis was performed. The time series showing a statistically significant linear trend were detrended before correlation analysis.

Results

Stock size

The biomass of the capelin stock shows considerable variation over the study period (Figure 2). The stock was 4–8 million tonnes in the 1970s and the early 1980s, and in the early 1990s. Since then it has been lower, reaching 4 million tonnes only in 2000 and 2008. It collapsed (declined to below 1 million tonnes as estimated during the autumn acoustic survey) three times during the period, in 1985, 1993 and 2003, and each collapse lasted for 4–5 years.

Ocean temperature and the area available for dispersal during summer

The Fugløya–Bear Island (FB) temperatures show large variations during the period 1972–2010 (Figure 3). The early 1970s were relatively warm, but the temperatures rapidly declined and reached a minimum in the late 1970s/early 1980s. Since then there has been an increasing temperature trend, although with interruptions of colder periods. Up to the early 1990s there were well-defined alternating warm and cold periods, but thereafter the temperature has been high, only interrupted by a few

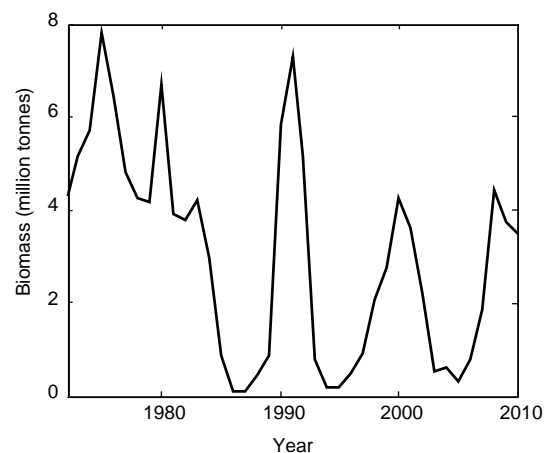


Figure 2. Temporal variability of the capelin stock biomass estimated from acoustic measurements.

moderately cold years in the late 1990s. Since 2000 the temperatures became very high, and most of the years in the last decade have had temperatures as high as, or higher than, during the former warm periods after 1972. However, during 2006–2010 the temperatures have decreased.

Despite being approximately 6°C lower, the temperature in the northeastern BS (NE temperature) varies in phase with the FB temperature (the year before) up to the late 1990s (Figure 3). In the late 1970s/early 1980s the NE temperatures were low (−1.6°C), but since the 1990s all years have had temperatures above −1°C. Maximum temperature was observed in the mid-1990s and there has not been a rising temperature trend in this region over the last decade. The opposite situation occurred in the north-western area (NW temperature) where the early and mid-1990s had close to average temperatures (−1 to −0.5°C) followed by a profound temperature increase of almost 2°C from 1995 to 2000.

Large interannual variability, and a pronounced increase in the area available for dispersal, is evident in the SOWI from the early 1990s (Figure 3). Since 2000, the index has been high (large ice-free areas during summer) most years, although with a low index (large ice-cover) in 2003 and 2008.

Ambient temperature (the preferred temperature range)

Capelin stay in water with temperatures from below −1.5°C up to almost 7°C (Figure 4a). However, 77% of the capelin individuals reside in waters having temperature $-1^{\circ}\text{C} < T < 3^{\circ}\text{C}$, although this range covers only 55% of the temperatures available

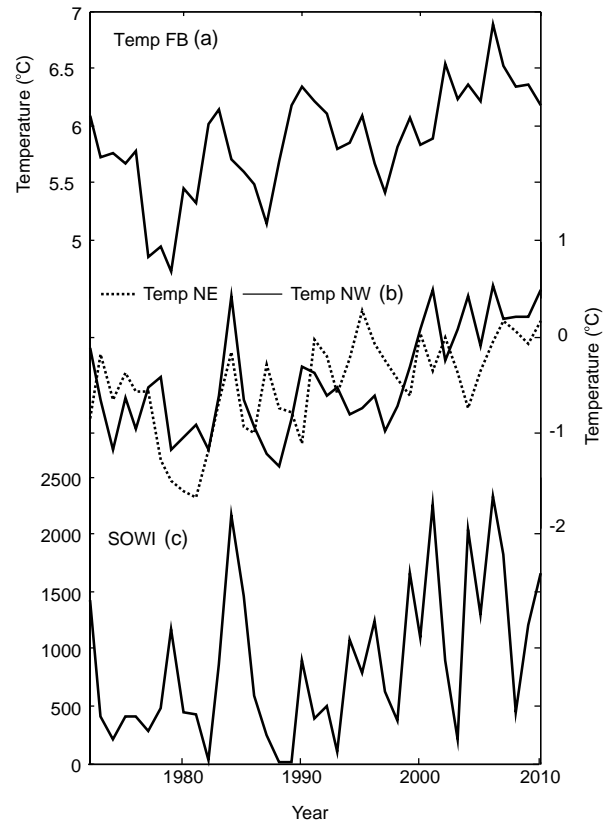


Figure 3. Temporal variability for the period 1972–2010 of the temperature series for the (a) Fugløy-Bear Island (FB) section and (b) the NE and NW regions of the BS and of (c) the summer open water index (SOWI).

to the fish, indicating that this temperature interval is preferred by capelin. The area of waters having the preferred temperature range shows strong interann-

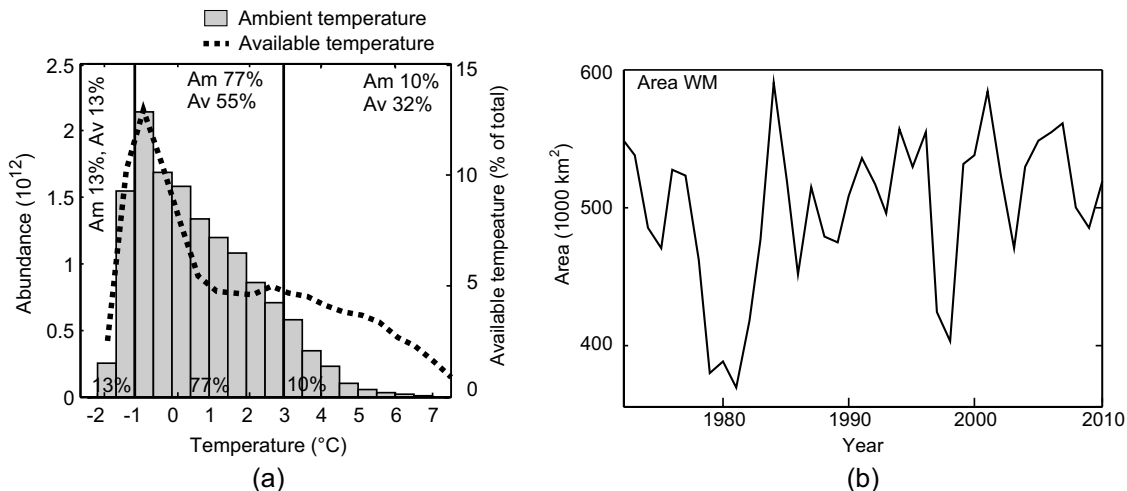


Figure 4. (a) Number of individuals plotted against their individual ambient temperature (bars) and distribution of temperatures available to the fish (dashed line, vertical axis on the right) for the period 1972–2010. Am gives the percentage of the individual ambient temperature distribution within the temperature ranges ($T \leq -1^{\circ}\text{C}$), ($-1^{\circ}\text{C} < T < 3^{\circ}\text{C}$) and ($T \geq 3^{\circ}\text{C}$), while Av gives the percentage of available temperature distribution within the same temperature intervals. (b) Temporal variability in area of water having the preferred temperature range ($-1^{\circ}\text{C} < T < 3^{\circ}\text{C}$). The calculation of the area was performed for the region between 72 and 80°N and between 20 and 60°E to ensure complete data coverage each year. Consequently, this time series should be considered an index series.

ual variability but no significant trend over the study period (Figure 4b). Both minimum and maximum temperatures occurred within a few successive years in the early 1980s.

Capelin distribution

In at least 75% of the years between 1972 and 2010 capelin were present over a large area in the BS (Figure 5a). Capelin were found north to about 79°N and eastwards to about 55°E in 25% of all the years. During years with capelin stock below 1 million tonnes the distribution was mostly restricted to the southern BS, and also more variable (no areas where capelin was present in 75% of these years, Figure 5b). When the stock was above 1 million tonnes, on the other hand, capelin spread widely in the BS, and the main expansion was towards the north and east (Figure 5c). The centre of mass of the distribution (CMD, black dots in Figure 5) reveals pronounced geographical differences between years, but the overall pattern is further south during the years with stock below 1 million tonnes.

There is a strong co-variability between capelin biomass and distribution area ($r = 0.68$, $P < 0.001$) and between biomass and CMD_Y ($r = 0.64$, $P < 0.001$) on interannual time scales (Figures 6 and 7). Thus, when the stock is large the CMD_Y is shifted northwards and the distribution area expands. The linear relation implies a northward CMD shift of 39 km, and an expansion of the distribution area by 35,000 km², associated with each 1 million tonnes increase in capelin biomass (Figure 7). In the late 1990s there was a shift in the time series. The co-variability remains, but the capelin distribution has been wider and CMD_Y further north when the stock has been moderate or low compared to earlier.

Due to the strong linear correlation between capelin biomass and distribution area and CMD_Y , the effect of stock size on these variables was removed by linear regression (Figure 7a,b). The pronounced shift in the late 1990s is clearly evident in the residual time series (Figure 7c). The cumulative correlation between the residual distribution area and the FB temperature (the year before) shows a gradual decrease throughout the study period, while there is a sudden drop in the correlation coefficients with the NE temperature and the WM_{area} (area of water with temperatures within the preferred temperature range) in the mid-1990s (Figure 8). For all three factors, the relationship changed from significant to insignificant in the mid-1990s. This implies that interannual variations in the ocean temperatures were an important driver for the capelin distribution area before the mid-1990s, but

thereafter the impact was significantly reduced. The correlation between the residual distribution area and the NW temperature are weaker, but stable, and no sudden change or shift occurred during the study period. The cumulative correlation between distribution area (not residuals) and stock size was varying

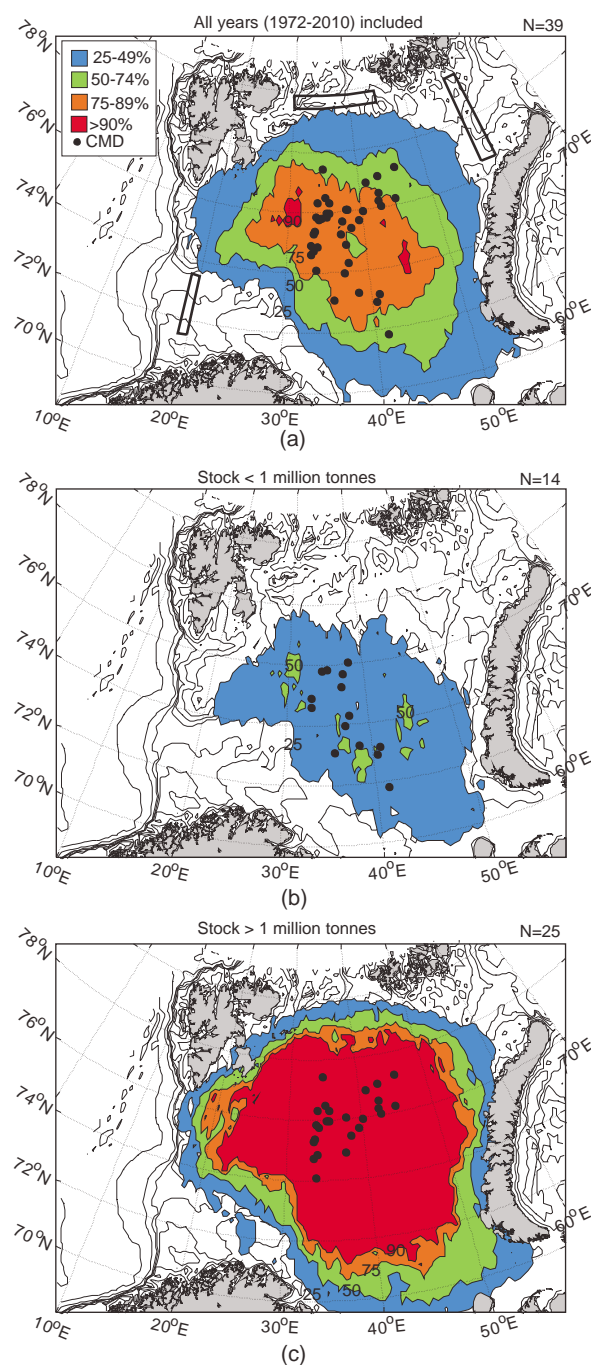


Figure 5. Capelin present/absent distribution in September–October 1972–2010: (a) for all years; (b) for years when the stock was < 1 million tonnes; and (c) for years when the stock was > 1 million tonnes. Contoured values are the number of years (in percentage of the total number of years N included) when capelin is present in each grid cell. The black dots show the centre of mass of the distribution (CMD).

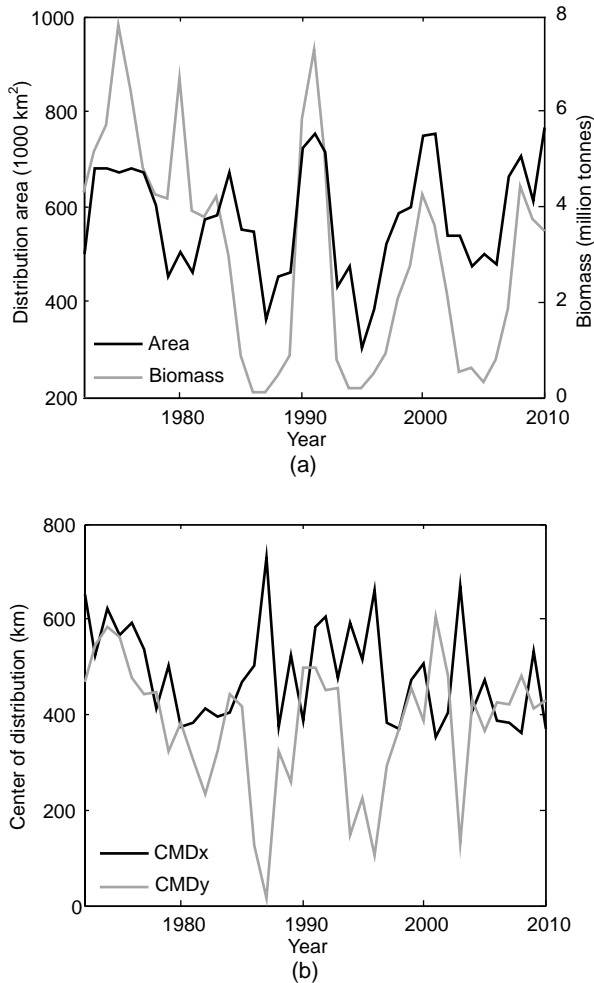


Figure 6. Temporal variability in (a) capelin distribution area and (b) centre of mass of the distribution in the zonal (CMD_x) and meridional (CMD_y) direction for the period 1972–2010. The capelin biomass is redrawn from Figure 2a.

and not statistically significant before ~ 1990 , but strong and stable thereafter.

Variations in the CMD_y are influenced by the NW temperature, the area available for dispersal during

summer (SOWI) and stock size (Figure 9). There is no sudden shift in the relation to the temperature as observed for the distribution area. The relation to the SOWI is weaker and changes over time, and is only statistically significant after 2003–2004. The relation between the CMD_y (not residuals) and the stock size show the same pattern as did the distribution area.

Discussion

The results of this and earlier studies show a strong link between the capelin distribution area and the stock size. The mechanism involved is likely to be that when the stock increases, the higher food demands are met by an expansion of the feeding areas (Gjøsæter 1999). Because the main focus of this study was to investigate the impacts of ocean temperature and ice variability on the distribution area, we adjusted for the stock size effect using a linear regression (Figure 7a,b). Such density effects are probably most important when the stock is large, because at small stock sizes there is probably no food limitation, and in such cases there is no need to spend energy by extending the feeding migration beyond what is needed to obtain the necessary food. While the expansion of the stock at higher stock sizes may not be a completely linear response, the results still suggest that this assumption is reasonable.

Although not specifically included in this analysis, the age composition may also be important for the capelin distribution. A stock consisting mainly of young capelin will have a more southerly distribution and a different migration pattern compared to a stock with a high abundance of older fish (Gjøsæter 1999; Fauchald et al. 2006). Thus, due to large interannual variations in the age-group abundances (Gjøsæter et al. 1998), the capelin distribution may vary considerably according to the age composition. However, as a large stock normally implies a large range of age- and size-groups and hence also

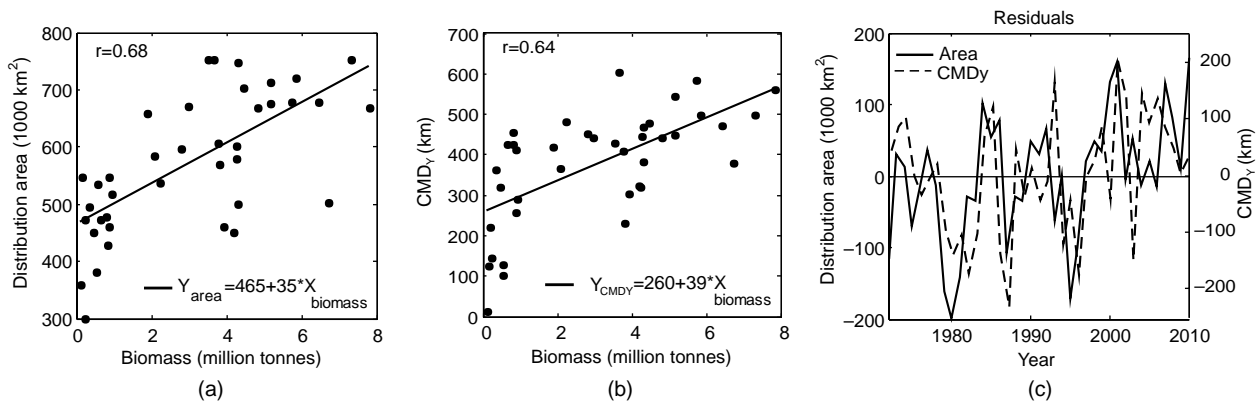


Figure 7. Distribution area versus (a) stock size and (b) CMD_y. The solid black line is the linear regression between the time series. Time series of the residuals from the linear regressions in (a) and (b) are shown in (c).

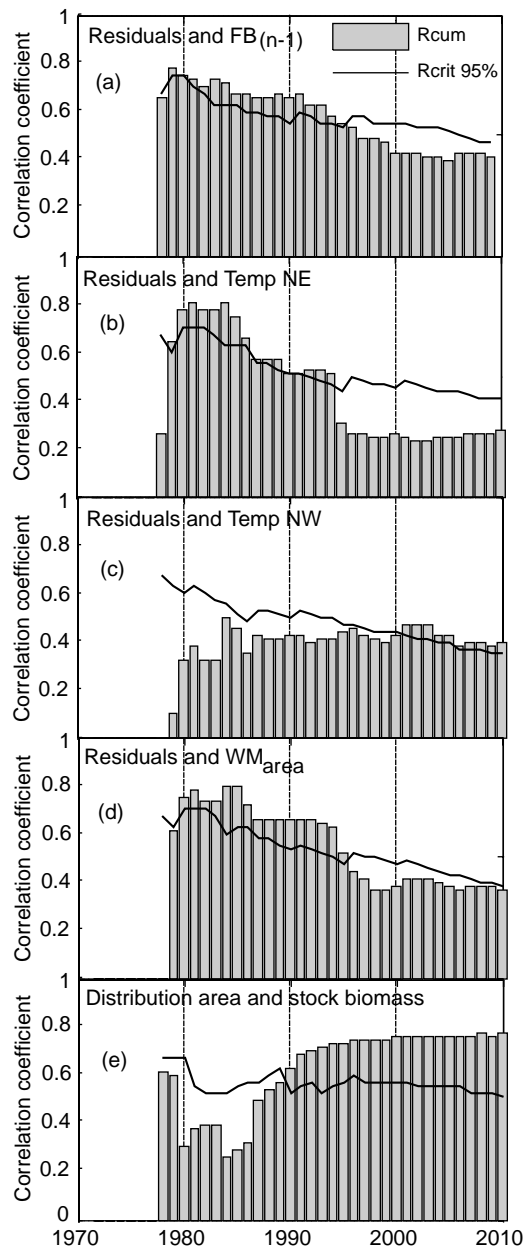


Figure 8. Cumulative correlation coefficients between distribution area residuals and (a) temperature at Fugløya–Bear Island the previous year, temperature in the (b) NE and (c) NW, and (d) area of water with temperatures within the preferred temperature range. (e) Cumulative correlation coefficients between distribution area (not residuals) and the capelin stock size.

considerable amounts of older fish (Gjøsæter et al. 1998), the effect of age composition is at least indirectly included in our analysis.

Interannual variability

Temperature is considered the most pervasive environmental factor that limits the temporal and spatial distribution, and governs the migratory behaviour of marine fish (Christiansen et al. 1997).

The individual ambient temperature will affect various physiological processes including growth of the fish (Brett 1979; Jobling 1994) and on physiological grounds it is likely that capelin will attempt to reside in waters according to a thermal preference. The results of this study indicate that this thermal preference for capelin is $-1^{\circ}\text{C} < T < 3^{\circ}\text{C}$. Still, capelin will sometimes stay in waters having temperatures outside the preferred temperature range, reflecting that the thermal preference may vary with various non-thermal components, such as food availability, nutritional state, body size, age, and maturity stage (Christiansen et al. 1997). The temperature in the northeastern and northwestern BS varies across the lower boundary of the thermal preference (Figure 3). Thus, in the northern regions the temperature (and the associated zooplankton production as described below) can restrict the capelin distribution.

We also found that the high-concentration areas of capelin are shifted northwards when the ice edge is far north during summer (evident as the positive correlation between CMD_Y and SOWI , Figure 9). When the ice edge is far north, the phytoplankton and zooplankton blooms in the marginal ice zone continue into August–September, which results in a potentially longer feeding season for capelin (Orlova

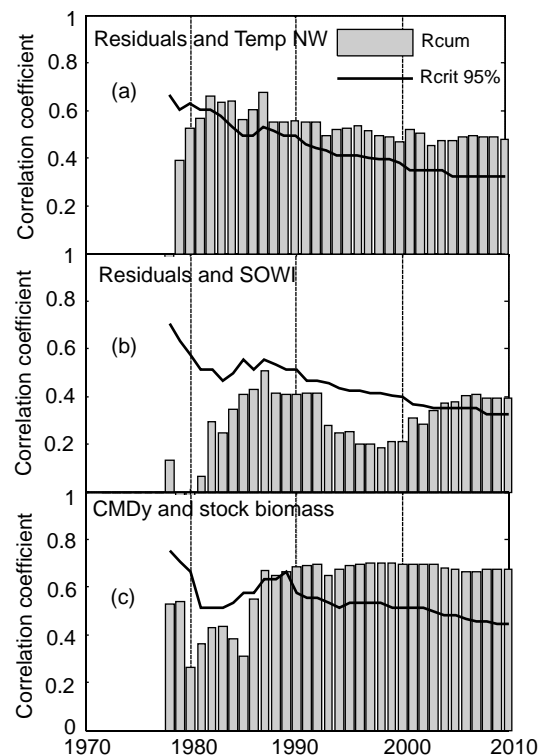


Figure 9. Cumulative correlation coefficients between the CMD_Y residuals and (a) temperature at NW and (b) the open water index (SOWI). (c) Cumulative correlation coefficients between the CMD_Y (not residuals) and the capelin stock size.

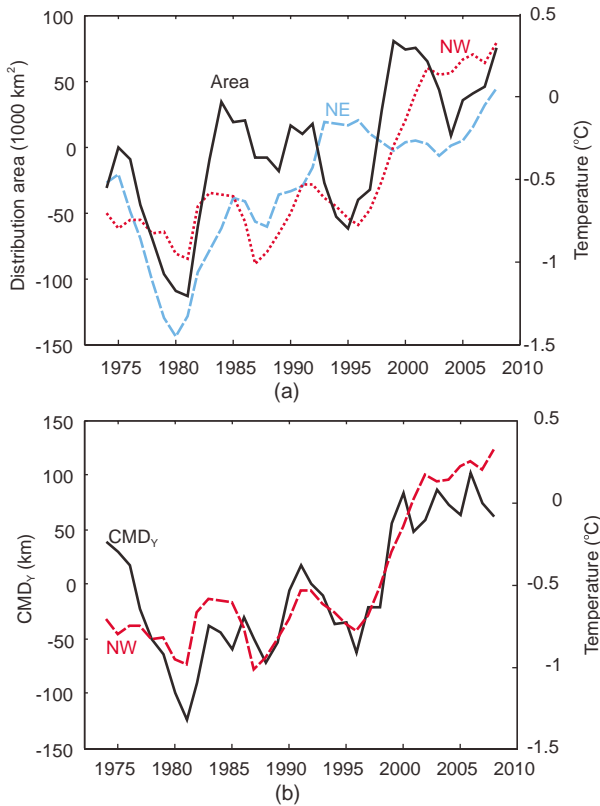


Figure 10. Five-year moving average (plotted against the mid-point) of temperature and (a) distribution area residuals and (b) CMD_Y residuals.

et al. 2005). Additionally, the biomass of the Arctic species *Calanus glacialis*, a major prey for capelin in northern areas, increases with ice melting (Orlova et al. 2005; Dalpadado & Mowbray 2013). Thus, more open water during summer can give better feeding conditions for capelin in the northern BS.

Because the amount of open water (the area available for dispersal) and the temperatures in the northwestern BS are inter-related ($r = 0.64$, $P < 0.001$), this study cannot distinguish between their effects. However, although ice cover and temperature are not independent of each other, they might have independent impact on the migration and distribution because different mechanisms are involved.

In fact, also the link between the ocean temperatures and the capelin is probably first of all an indirect effect, strongly connected to the link between the temperature and zooplankton production and distribution (Gjøsæter 1998 and references therein). The abundance of *Calanus finmarchicus*, the most dominant zooplankton in the BS, is closely related to the supply of warm Atlantic Water flowing from the Norwegian Sea (e.g. Skjoldal et al. 1992). High temperatures can therefore be an indication of higher zooplankton abundance in the Atlantic and

Arctic Water (Orlova et al. 2005, 2010), and hence for better capelin growth (Gjøsæter & Loeng 1987; Gjøsæter 1999; Gjøsæter et al. 2002). Thus, high temperature will be a proxy for larger areas having temperatures within the preferred temperature range, higher food supply and better growth conditions. This study does not distinguish between the direct and indirect effects.

Fauchald et al. (2006) concluded that ocean temperature and ice cover only had a marginally positive relationship on the horizontal displacement of capelin. However, they did not adjust for the stock size effect before comparing with temperature/ice and they investigated distribution shifts along a southwest–northeast axis. Our results showed a strong relationship between stock size and distribution, and that the main effect of temperature/ice on the capelin distribution is in the meridional direction (CMD_Y). Hence, the effect of the environment is likely to be masked if the stock size effect is not accounted for and shifts along other axes (than meridional) are considered. Linear regression analysis on our time series over the study period 1970–2010 reveals that 46% of the interannual variability in capelin distribution area is explained by the stock size alone. Including temperature/ice add 20% to the explanatory power of the regression. Hence, 66% of the interannual variability in the capelin distribution area is explained by the combined effect of stock size and temperature/ice.

Long-term changes and shifts

Our results show a sudden shift in the capelin series (Figure 6), and in the interannual variability between the distribution area and the ocean temperatures (Figure 8), happening in the mid/late 1990s. At the same time, the temperature in the northeastern BS increased from suboptimal to optimal (Figure 3). Thus, before the mid/late 1990s the temperatures in the northeastern area represented a constraint for the capelin, and the capelin responded to the increasing/decreasing temperatures by expanding/contracting the distribution area (Figure 10a).

However, after the mid/late 1990s, the temperatures have been optimal in the entire northern BS, which supports a widespread capelin distribution. Consequently, after the mid/late 1990s the temperature variations in the northeastern BS were not followed by corresponding changes in the capelin distribution (Figure 10a). Instead, the capelin distribution in this period varied in synchrony with the temperatures in the northwestern BS (Figure 10a). As discussed in above, the rapid temperature rise in the northwestern areas after the mid/late 1990s, in combination with more open water and

more food, should have given better conditions for capelin in this area. Consequently, capelin responded by expanding its feeding area northwards. In this respect it should be noted that the wide distribution of the stock during the last collapse (2003–2006) could partly be related to the fact that this collapse was not as severe as the two former ones (Gjøsæter et al. 2009). Thus, the higher abundance of two-year-olds relative to the former collapses can partly explain the more northerly distribution. On the other hand, the northward location of the high-concentration areas (the CMD_Y) shows a strong relation to temperature in the northwestern areas over the entire period (Figure 10b), adding support to the result that the temperature variation is the main factor causing the observed shift in the mid/late 1990s.

Over the study period, the temperature increased by 1.0–1.5°C in the northwestern and northeastern BS (Figure 3). Our results indicate that an increase of about 1°C will lead to an increase of about 125,000 km² of the distribution area and a ~150 km northward shift of the high-concentration areas (Figure 10). This is consistent with Rose (2005), who argued that a temperature change of this size should be accompanied by a change in the capelin distribution of several hundreds of kilometres. However, comparable impacts are obtained if the capelin stock size increases with ~4 million tonnes (Figure 10). Thus, to give reliable projections of temperature/ice-induced changes in the capelin distribution, the factors influencing the stock size (prey, predators, trophic interactions) must be included.

Possible effects of changes in the capelin distribution

After the shift in the mid/late 1990s, capelin have been distributed widely in the BS although the stock abundance has been moderate or low, and this might have had impacts both on the capelin stock and on other species in the BS. The overall lower capelin density might have increased the food availability for the young capelin, and possibly also decreased the predation from cod and other predators.

An investigation of the ecosystem impacts of the capelin distribution changes is beyond the scope of this study, but should be carried out in future. For instance, the northward shift of the high-concentration capelin areas might have been one (out of several) of the factors causing an observed northward distribution of cod (ICES 2011; Johansen et al. 2013) and baleen whales (Skern-Mauritzen et al. 2011) during the last decade. In the southern BS the shift should cause decreasing capelin predation on zooplankton, and an increase in euphasiids (krill), which possibly is linked to reduced predation from

capelin, has been observed in the southern areas during the last years (Johannesen et al. 2012).

Summary and conclusions

One biotic (stock size) and two abiotic (ocean temperature and ice) factors have been found to impact on the migration and spatial distribution of capelin near the end of the feeding season. Those factors are not independent of each other, but they seem to influence the migration and distribution in independent ways. Our study shows that the abiotic factors set the large-scale limits for the capelin distribution, while stock size (and probably age structure) determines how capelin use the available areas.

More specifically:

- The distribution of capelin depends on the combined effect of stock size and ocean temperature/ice cover in the northern BS. An increase in stock size of 4 million tonnes and a temperature increase of 1°C give comparable impacts on the distribution.
- Since the mid/late 1990s, the capelin have been distributed widely and the high-concentration areas have shifted northwards, although the stock size has been small or moderate. This seems to be caused by the high temperatures and low ice cover observed during the period.

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