

Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change

Svein Sundby and Odd Nakken

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Arcto-Norwegian cod tend to produce strong year classes in warm years and poor year classes in cold years. This work shows that spawning intensity at various spawning sites along 1500 km of Norwegian coast is also influenced by climate variations. However, while the recruitment response to temperature is immediate and on an interannual time-scale, the response to changes in spawning site is slower, on a multidecadal time-scale. There have been two cold and two warm periods during the 20th century, cold from 1900 to 1920, warm from 1930 to 1950, cold from 1960 to 1970, and warm since the mid-1980s. A time-series for 1900–1976 on cod roe indices along the coast shows that the southernmost spawning areas are more important during cold periods, and the northernmost ones in warm periods, and coincide with high population fecundity. After 1976, qualitative observations show that there have been poor spawning fisheries in the southernmost spawning areas during the present warm period. From 2003, spawning has been observed along the coast of East Finnmark where it did not transpire during the previous 40 years.

Keywords: Arcto-Norwegian cod, Atlantic multidecadal oscillation, climate effects, spawning areas.

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S. Sundby and O. Nakken: Institute of Marine Research, PO Box 1870, Nordnes, N-5817 Bergen, Norway. S. Sundby: Bjerknæs Centre for Climate Research, Allégaten 55, 5007 Bergen, Norway. Correspondence to S. Sundby: tel: +47 55238468; fax: +47 55238687; e-mail: svein.sundby@imr.no

Introduction

The Arcto-Norwegian cod¹ is an Arcto-boreal cod stock found in the colder part of the habitat range of Atlantic cod (*Gadus morhua*) stocks. Only the West Greenland cod and the northern cod off Newfoundland are found at lower temperatures (Sundby, 2000) (Figure 1). A general feature of Arcto-Norwegian cod is that it tends to produce strong year classes in warm years and poor year classes in cold years (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989). This feature has also been shown to be valid for the other Atlantic cod stocks in the lower temperature range (deYoung and Rose, 1993). In contrast, cod stocks in the upper temperature range (such as North Sea cod and Irish Sea cod) respond with poor year classes in warm years and good year classes in cold years (Ottersen, 1996; Planque and Fox, 1998; Planque and Frédou, 1999). This particular temperature response of Atlantic cod stocks indicates that temperature, in addition to its direct effect on recruitment (i.e. rapid growth through the most vulnerable life stages), is a proxy for other processes important to recruitment, such as the supply of prey items by advection of copepods (Sundby, 2000).

For Arcto-Norwegian cod, temperature has been documented as influencing the entire life history in a number of ways. Maturation and egg production of individual fish depend on feeding conditions which, in turn, are related to prey abundance and temperature (Kjesbu *et al.*, 1998). Pelagic juveniles in the warmer, western parts of the Barents Sea grow faster than those in the colder, eastern areas (Bjørke and Sundby, 1986; Suthers and Sundby, 1993), a feature that has been reproduced by modelling larval and juvenile growth and transport (Vikebø *et al.*, 2005). Year-class strength and individual size of 0-group cod are positively correlated with ambient temperature (Nakken, 1994; Ottersen and Loeng, 2000). Interannual spatial temperature variations strongly influence the distribution and growth of young and immature cod (Nakken and Raknes, 1987; Ottersen *et al.*, 1998).

Timing and duration of spawning, however, have been considered to be invariant with varying temperature conditions. During the 1970s and 1980s, spawning periods were monitored at selected sites at the main spawning areas in Lofoten (Ellertsen *et al.*, 1989). Timing and duration were remarkably constant between years, starting at the beginning of March, peaking

¹The Atlantic cod stock with its nursery and feeding area in the Barents Sea and its spawning area along the Norwegian coast has been termed variously “Arcto-Norwegian cod”, “Barents Sea cod”, and “North-East Arctic cod”. Although “North-East Arctic cod” has been the official name used by ICES during the past 30 years or so, we avoid using this name because it is confusing, for two reasons. First, in an ecological sense, the fish stock is not an Arctic species, but an Arcto-boreal species mainly associated with Atlantic water masses of the Barents Sea and the coast of Norway, only occasionally migrating into Arctic waters during summer to feed on capelin. Second, “North-East Arctic” is a meaningless geographic description of the habitat of this stock, i.e. the Barents Sea, because this region is neither a northern nor an eastern part of the Arctic. “Barents Sea cod” is, in our opinion, a good description for this cod stock, but because this name has not been in official use, we here use the former official name used by ICES, namely “Arcto-Norwegian cod”.

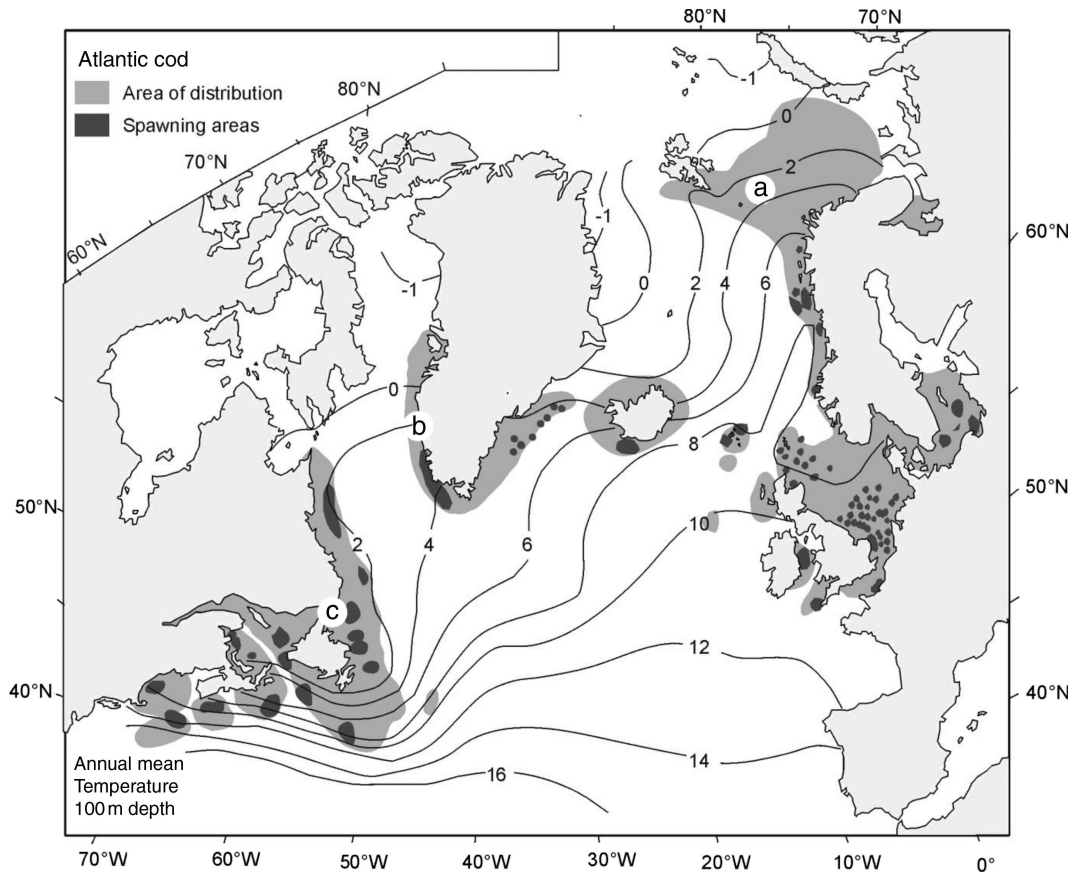


Figure 1. Distribution of Atlantic cod stocks and the ambient mean annual temperature (at 100-m depth). The three cod stocks at the low end of the temperature range are (a) Arcto-Norwegian cod, (b) West Greenland cod, and (c) northern cod (after Sundby, 2000).

during the first days of April, and terminating at the beginning of May. This interannual consistency in spawning period has been interpreted as an indication that the seasonal light cycle is the main trigger for spawning. Over a longer term, i.e. from 1929 to 1982, spawning changes and take place about two weeks later (Pedersen, 1984). That finding was based on data from the Norwegian fishery statistics by investigating the time of the fishing season when the land-based fishing industry stopped receiving cod roe for processing. There has been discussion whether this long-term change in peak spawning is linked to the similar long-term change in age at maturation. From the early 1950s to the 1990s, age at maturation decreased from ~ 10 years to 7 years (Jørgensen, 1990); it is currently 6.3 years (Nakken, 1994).

The areas along the southeastern border of the Lofoten archipelago in northern Norway have been known, at least since the ninth century (Egil's Saga, 1960), as the major spawning fishery location of *skrei*, the Old Norse term for Arcto-Norwegian cod. *Skrei* means "the wanderer", derived from belief that the fish migrate from far away (i.e. the Barents Sea) to spawn along the Norwegian coast; the term was used to distinguish these fish from local, coastal populations of cod. The *skrei* have an appearance different from coastal cod in colour, shape, otolith structure, and age at maturation (Rollefsen, 1933; Godø, 1984a). In addition to the central Lofoten spawning district, there are a number of other spawning locations of *skrei* along the Norwegian coast from western Norway to Finnmark (Sundby and Godø, 1994). Figure 2 shows

the locations of spawning areas along 1500 km of coast, from Sotra off Bergen to Sørøya in West Finnmark. The main spawning area has traditionally been at Lofoten, with secondary areas at Møre, south of Lofoten, and Senja and Malangsgrunnen, north of Lofoten, with minor spawning areas scattered at specific sites along the coast. Occasional spawning locations are mainly off-shore, where spawning is missed for a number of years but then intense for 2–3 years, as for example on Moskenesgrunnen and Eggagrunnen off Lofoten. Therefore, even if the Lofoten spawning district is definitely the most important spawning area, fewer than one-third of the *skrei* spawn there (Sundby and Bratland, 1987).

Sætersdal and Hysten (1964) analysed the catch statistics for the *skrei* spawning fisheries for a 90-year period from the 1860s to the 1950s. They observed large interannual variations in the catches, but also noticed a substantial long-term shift from higher catches in the southern location, Møre (Figure 2), before the 1930s, to higher catches in Lofoten thereafter. In the 1910s, catches in the southern locations exceeded catches in Lofoten in some years. The authors ascribed this development to "natural fluctuations", but also indicated that a changing fishing pattern might have been implicated.

During February and March of 2004 and 2005, the fishing industry reported large numbers of mature and pre-spawning cod at the fishing grounds along the coast of East Finnmark (hatched area in Figure 2), after an extended period of high temperature, i.e. from the start of the 1990s (Figure 3). This situation motivated closer inspection of historical fisheries statistics to

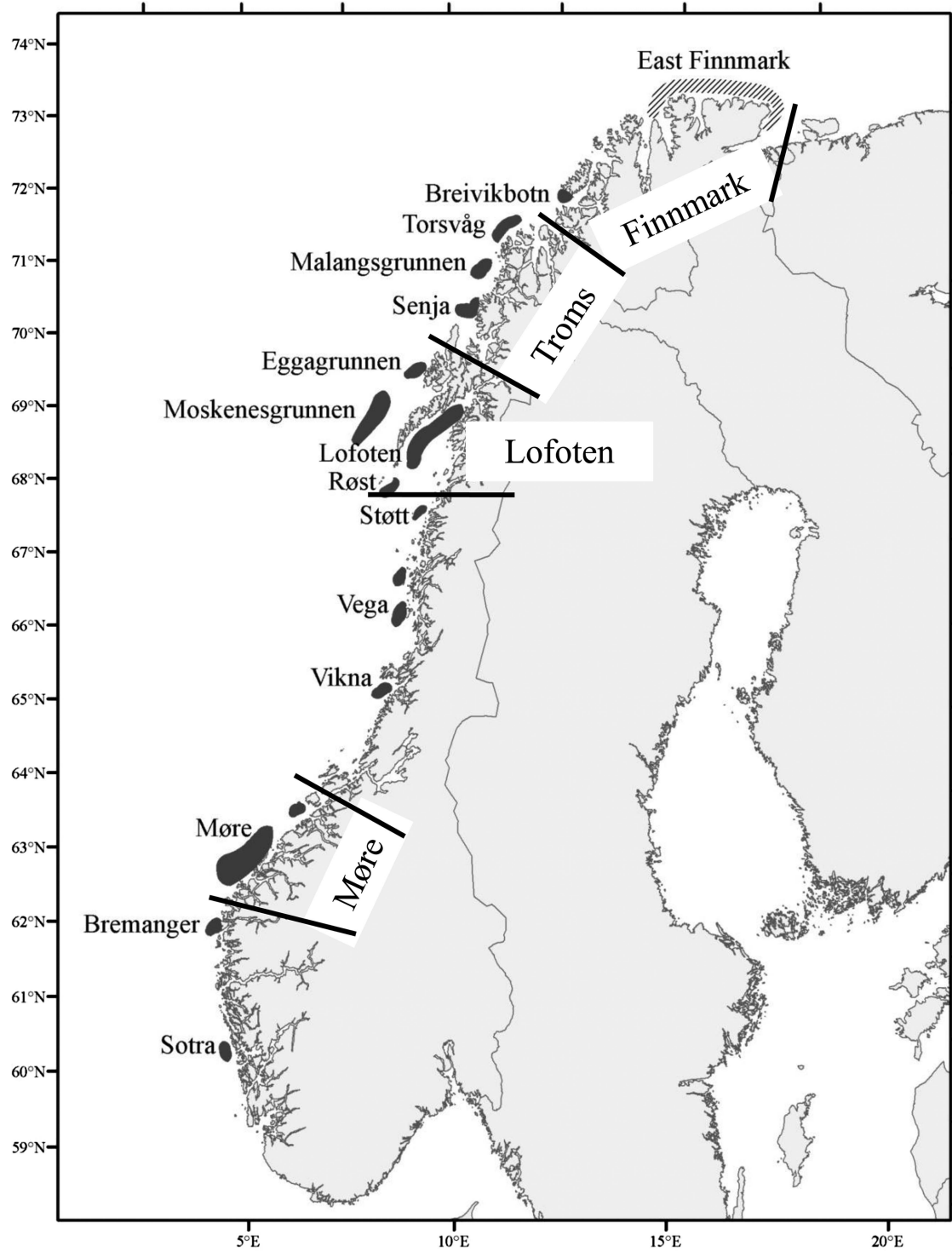


Figure 2. Spawning areas of Arcto-Norwegian cod (after Sundby and Godø, 1994). The data on roe index, F_{Ni} , here are aggregated for the four spawning districts Møre, Lofoten (which consists of the four spawning areas Lofoten, Røst, Moskenesgrunnen, and Eggagrunnen), Troms (which consists of the three spawning areas Senja, Malangsrunden, and Torsvåg), and Finnmark (which consists of the spawning area Breivikbotn and from East Finnmark to the Russian border). The hatched area along the coast of East Finnmark indicates the region where there has been a spawning cod fishery since 2003.

explore whether there had been similar situations during earlier periods, particularly during the previous long-term trend of warmer temperatures from the 1930s to the 1950s. Here, we address the issue of long-term changes/oscillations in spawning

intensity at the southern and northern *skrei* spawning locations along the Norwegian coast during the 20th century. We investigate whether these variations are correlated with similar long-term changes/oscillations in the marine climate of the northeastern

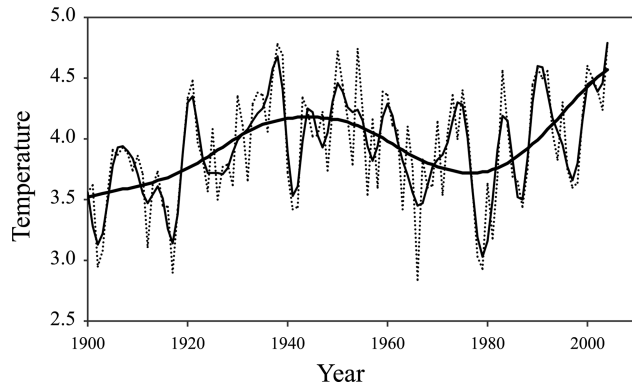


Figure 3. Time-series 1900–2005 of temperatures for the Atlantic water masses of the Kola section in the Barents Sea. Dotted line, annual mean temperatures; solid thin line, 5-year running mean temperature; heavy solid line, annual mean temperatures with a 30-year low-pass filter applied.

North Atlantic, and discuss possible mechanisms behind such a correlation.

Material and methods

An egg production index time-series for *skrei* was published annually in the fisheries statistics of “Norges fiskerier” (Norwegian Fisheries) issued by the Directorate of Fisheries during the period 1900–1940. It was based on commercial catches of *skrei* during the spawning season (February–May) from all local fishing harbours along the whole coast of Norway. This seasonal spawning fishery, the traditional way of harvesting Barents Sea cod, has a documented history of 1200 years (Egil’s Saga, 1960). Here, we aggregate the egg production index and present it for four major spawning regions (Figure 2). The southern district is “Møre”, the central district “Lofoten” (consisting of Lofoten, Røst, Moskenesgrunnen, and Eggagrunnen; Figure 2), and the two northernmost districts are “Troms” (consisting of Senja, Malangsgrunnen, and Torsvåg; Figure 2), and “Finnmark” (including Breivikbotn and northeastward to the Russian border; Figure 2). The tabulated egg production index, which we term the roe index, F_N , is defined as

$$F_N = \frac{R}{N_C}, \quad (1)$$

where R is the total litres of cod roe delivered to the region during the entire fishing season at the spawning sites, and N_C is the corresponding number of cod (in 1000s) delivered. During the period 1935–1952, the fisheries statistics changed the definition of the index to be based on weight of cod instead of numbers. Hence, the new index, which we term F_W is defined as

$$F_W = \frac{R}{W_C}, \quad (2)$$

where W_C is the tonnage of gutted cod delivered during the entire spawning season. We used the overlapping period of six years from 1935 to 1940 for the two indices to derive the original index F_N from F_W .

The regression line for the southern and northern spawning districts (Møre, Troms, and Finnmark) was

$$F_N = 2.49F_W + 14, \quad (3)$$

with a correlation coefficient of $r^2 = 0.93$. For the central spawning region Lofoten, the correlation was somewhat different:

$$F_N = 3.27F_W - 3, \quad (4)$$

with a correlation coefficient of $r^2 = 0.82$.

From 1953 to 1970, the roe index was no longer tabulated in the statistics, but the basic data on roe and fish were still available. Therefore, the F_W index was constructed from the tabulated tonnages of roe and *skrei* received and transformed to F_N using the above regressions. From 1970 to 1976, the statistics no longer separated *skrei* and coastal cod. Hence, the last 7 years of the time-series is not reliable for the Møre district because most of the cod delivered there was coastal cod. In the northern districts, however, most of the landings remained as *skrei*, so the index can still be used for those regions until 1976, although with less precision. In 1977, “Statistisk sentralbyrå” (the agency Statistics Norway) took over the publication of the fisheries statistics from “The Directorate of Fisheries”. Since then, the data on cod roe have not been published.

The index can be considered as a population fecundity index for each spawning area. The spawning–stock biomass consists of a number of age classes and lengths. The large range of variation in individual fish fecundity is not only a function of length and age, but also of condition factor (Marshall *et al.*, 1999). A typical first-time spawner ~ 60 cm in length would produce 0.5–1.0 million eggs, whereas an old multiple-spawner ~ 120 cm in length would produce 10–12 million eggs (Kjesbu *et al.*, 1998). As the roe index sums the total quantity of fish, both males and females, it does not take account of possible changes in sex ratio throughout the time-series. The fishing period is limited because the *skrei* arrive at the spawning sites in February and disappear in late April/early May on their way back to the Barents Sea. As the spawning fishery has been conducted with small vessels, the fishing operations and their outcome have always been highly dependent on weather. Hence, the egg production index is a better measure for spawning intensity than catch biomass.

Climate data are taken from the Russian Kola section (Tereshchenko, 1997), which represents well the interannual variations in the thermal climate of the entire region of spawning cod (Sundby, 1994). Temperatures are annual means of the Atlantic water in the mid-part of the section, i.e. station numbers 4–7 at 50–200 m depth for the period 1900–2005.

Results

Figure 4 shows the annual values of the roe index, F_N , for the central spawning district of Lofoten (upper panel), for the southern district Møre, and for the two northernmost districts Troms (Senja, Malangsgrunnen, and Torsvåg) and Finnmark (Breivikbotn to the Russian border) (lower panel). Interannual variations are large for all spawning districts, typically 50–100%. There are, however, long-term trends in the data, which are opposite in the southern and northern districts. In the period 1930–1950, there is a pronounced maximum in the roe index in the two northernmost spawning regions, whereas the index is at a

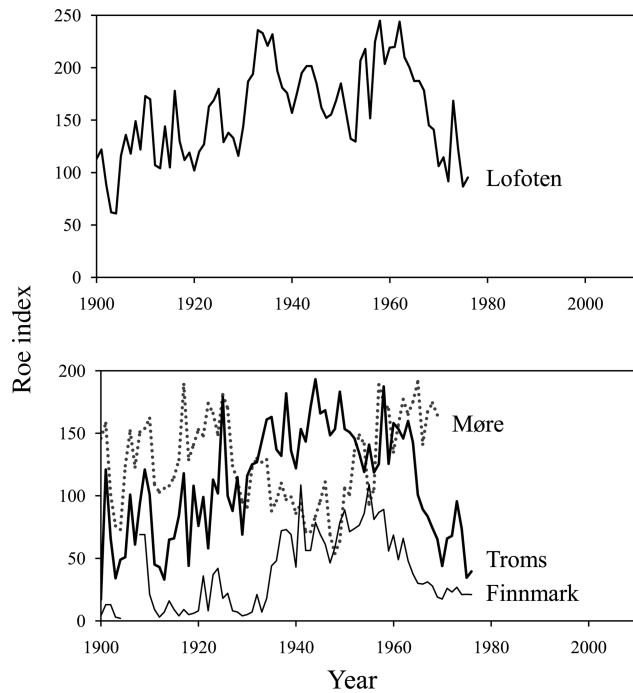


Figure 4. Time-series 1900–1976 of the annual values of roe indices, F_N , for the central spawning district Lofoten (upper panel) and the southern spawning district Møre and the two northernmost spawning districts Troms and Finnmark (lower panel).

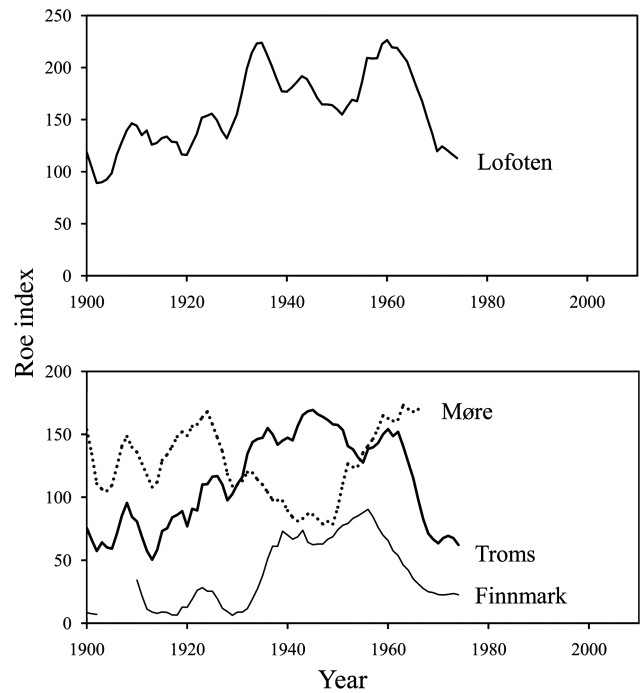


Figure 5. Time-series 1900–1976 on the five-year running mean values of roe indices, F_N , for the central spawning district Lofoten (upper panel) and the southern spawning district Møre and the two northernmost spawning districts Troms and Finnmark (lower panel).

minimum in the southernmost region (Møre) during the same period. The long-term trend for the central spawning district Lofoten is somewhat different from the other districts, with two dominant peaks, one in the late 1930s and the other in the 1950s.

The long-term opposite trends of the southern spawning district Møre compared with the two northernmost districts Troms and Finnmark stand out more clearly as 5-year running means, shown in Figure 5 for the Lofoten district (upper panel) and for the southern spawning district Møre and the two northern districts Troms and Finnmark (lower panel).

Figure 3 shows the temperature time-series from the Atlantic water of the Kola section depicted as annual means, 5-year running means, and annual means with a 30-year low-pass filter applied. Apart from the interannual variations (dotted line), there is, at certain times, a predominant decade-scale period associated with the North Atlantic Oscillation Index (Hurrell *et al.*, 2003). The 30-year low pass filter emphasizes the multidecadal temperature signal of the North Atlantic described by Sutton and Hodson (2005).

The long-term increase in the roe index in the northern spawning districts from the 1920s to the 1930s and the decrease from the 1950s to the 1970s seem to be correlated with long-term trends in sea temperature. The inverse trends of the roe index for the southern district Møre demonstrate a negative correlation with temperature. In the northernmost spawning district Finnmark, where the temperature is lowest, the duration of the period of high roe index in the mid-20th century is ~ 10 years shorter than in the other northern district Troms; the increase came later than in Troms, and the decrease started earlier.

Figure 6 shows the linear regressions between 5-year running mean temperatures and the 5-year running mean roe indices. The running mean point of the temperatures is the mean of the

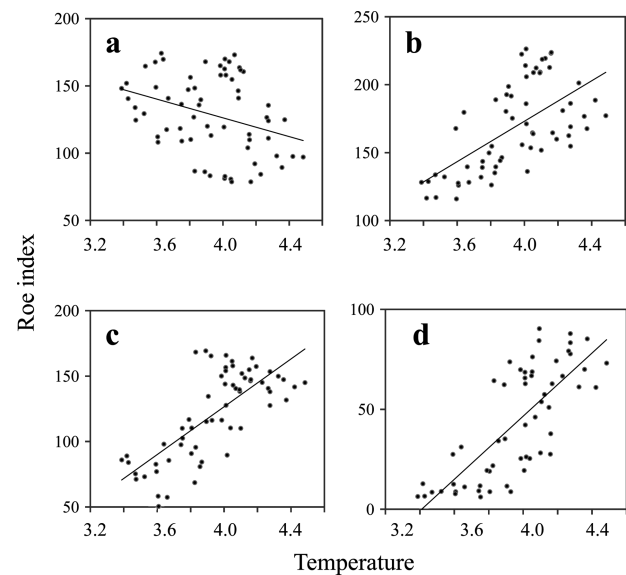


Figure 6. Linear regressions of five-year running mean temperature and five-year running mean roe index, F_N , for the four spawning districts: (a) Møre ($r = -0.33$, slope -34.9), (b) Lofoten ($r = 0.62$, slope 74.5), (c) Troms ($r = 0.73$, slope 91.3), and (d) Finnmark ($r = 0.76$, slope 79.0).

5 years prior to the point. This is done because the roe indices are assumed to be influenced by the past growth conditions for mature cod. The southern district Møre (Figure 6a) is the only spawning location where the correlation coefficient between the roe index and temperature is negative ($r = -0.33$, slope is

–34.9). For Lofoten (Figure 6b), the correlation is positive, with a higher correlation coefficient ($r=0.62$, slope is 74.5). The two northern districts Troms (Figure 6c) and Finnmark (Figure 6d) have the highest positive correlation coefficients, with $r=0.73$ (slope is 91.3) and 0.76 (slope is 79.0), respectively.

After the last cool period in the Northeast Atlantic during the 1960s and 1970s, sea temperature started increasing again from the early 1980s, but the time-series on the roe indices were discontinued during the mid-1970s. Newspaper reports on the increasing *skrei* spawning fishery in eastern Finnmark after spring 2003 indicate that the stock is responding in a manner similar to how it did in the previous warming in the mid-20th century. During the 2007 spawning season, analysis of otoliths taken from cod caught at various spawning areas in the fjords and along the coast of East Finnmark showed that between 70 and 100% of the cod were *skrei* (interview with Kjell Nedreaas, Institute of Marine Research, in the newspaper *Fiskaren*, 2 June 2007).

Discussion

As mentioned above, high temperature is beneficial for the Arcto-Norwegian cod in many ways, because it increases egg production (Kjesbu *et al.*, 1998), recruitment (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989), juvenile growth rate, and abundance (Ottersen and Loeng, 2000; Vikebø *et al.*, 2005). The positive correlation between temperature and the roe index for the central spawning district Lofoten (Figure 6b) and the two northernmost spawning districts (Figure 6c and d) also demonstrates that population fecundity increases as spawning areas are displaced north. In other words, behind the positive correlation coefficients between temperature and roe index (Figure 6b–d), there are probably two factors, (i) northward displacement of spawning areas, and (ii) increased population fecundity, contributing to the same positive correlation. At the southern fringe of the spawning areas, i.e. Møre (Figure 6a), the two factors would have opposite responses to temperature change, because population fecundity there would also increase with increasing temperature, and local spawning intensity would decrease because a larger portion of the mature fish is moving north. The considerably lower absolute value of the correlation coefficient ($r = -0.33$) and lower absolute value of the slope of the regression line for Møre indicate that both of the two factors are embedded in the correlation, but that the decrease in the spawning intensity (attributable to the northward movement of cod) is the dominant of the two. Hence, Figure 6 indicates that Arcto-Norwegian cod responds to increasing temperature with both a northward displacement of its spawning areas and increased individual and population fecundity.

The increase in population fecundity of Arcto-Norwegian cod is also strongly correlated with the liver index and condition factor for the mature population (Marshall *et al.*, 1999). High condition factor and high spawning–stock biomass are associated with good feeding conditions for adult cod in the Barents Sea, which, in turn, are influenced by the overall productivity of the Barents Sea. The overall productivity of the Barents Sea increased with increasing temperature partly because of increased influx of copepod-rich Atlantic water from the Norwegian Sea (Skjoldal and Rey, 1989; Helle and Pennington, 1999), and partly because of increased habitat area for plankton production and fish stocks caused by the reduction in ice cover in the northern and eastern parts of the Barents Sea during spring and summer (Stenevik and Sundby, 2007).

Arcto-Norwegian cod are managed as a single stock unit, but the unit is distinguished by two components (proper Barents Sea, and Svalbard) that are geographically separated as immature fish (Trout, 1956; Maslov, 1972). It is assumed that fish from the two components mix during spawning. However, there are also indications through tagging experiments that fish from the eastern Barents Sea spawn mainly from Lofoten northwards, whereas the western component generally spawns more offshore and in the spawning areas south of Lofoten (Trout, 1956; Høyen *et al.*, 1961; Godø, 1984b, 1986; Godø *et al.*, 1984).

Recent observations of mature pre-spawning cod in the northernmost spawning district of Finnmark since spring 2003 indicate a repetition of increased spawning intensity observed during the previous warm period. Fishery statistics clearly reveal a similar period in the previous warm period of the mid-20th century, from about 1930 to the 1950s. The Troms spawning district (Senja, Malangsgrunnen, and Torsvåg), adjacent to Finnmark, displays a similar trend in spawning intensity. However, *skrei* spawning there have never been completely absent in the colder periods, and during recent years since *skrei* again started to spawn in Finnmark, the popular media is reporting record high catches of spawning *skrei* in Troms.

Also, in the central spawning district Lofoten, the long-term trend in spawning activity appears to co-vary with temperature, but the pattern there is somewhat different, with two peak periods, one at the beginning and one at the end of the warm period. The most remarkable result, however, is the inverse response to the climate trends in the southernmost spawning district Møre. This indicates that the Arcto-Norwegian cod stock responds to climate change by displacing spawning locations. When temperature increases, spawning is displaced north, whereas a reduction in temperature results in a southward displacement of spawning (Figure 7). The multidecadal temperature pattern is documented here by observations from the Kola section in the Barents Sea through the 20th century, but the temperature signal is not spatially limited to that region. Sutton and Hodson (2005) recently showed an extended time-series back to 1870 of multidecadal summer temperatures for the entire North Atlantic. They confirm the multidecadal pattern of the Kola section during the 20th century and moreover show that the last three decades of the 19th century were warmer than normal. Further, Gray *et al.* (2004) analysed tree rings from Europe and North America and found that the multidecadal temperature pattern was a dominant climate signal through their entire data series, which extended back to the mid-16th century. Hence, it would be anticipated that a *skrei* spawning migration response to multidecadal climate variation might have been present during past centuries.

Among the Atlantic cod stocks, the Arcto-Norwegian cod, together with the northern cod and West Greenland cod, is located at the lower range with respect to temperature habitats, as shown in Figure 1. Under such conditions, it is likely that an increase in temperature results in a northward expansion of habitat, because ambient temperatures are suboptimal in all regions of their habitat with respect to growth rates of larvae and juveniles (Otterlei *et al.*, 1999) and adults (Jobling, 1981), and to recruitment (Sundby, 2000). However, the reduction in spawning intensity at the southern (and warmest) edge of the spawning areas of Arcto-Norwegian cod indicates that the expansion of spawning in the north is at the cost of a reduction in the south. There are several possible mechanisms behind such a response, listed and defined in the three subsections below.

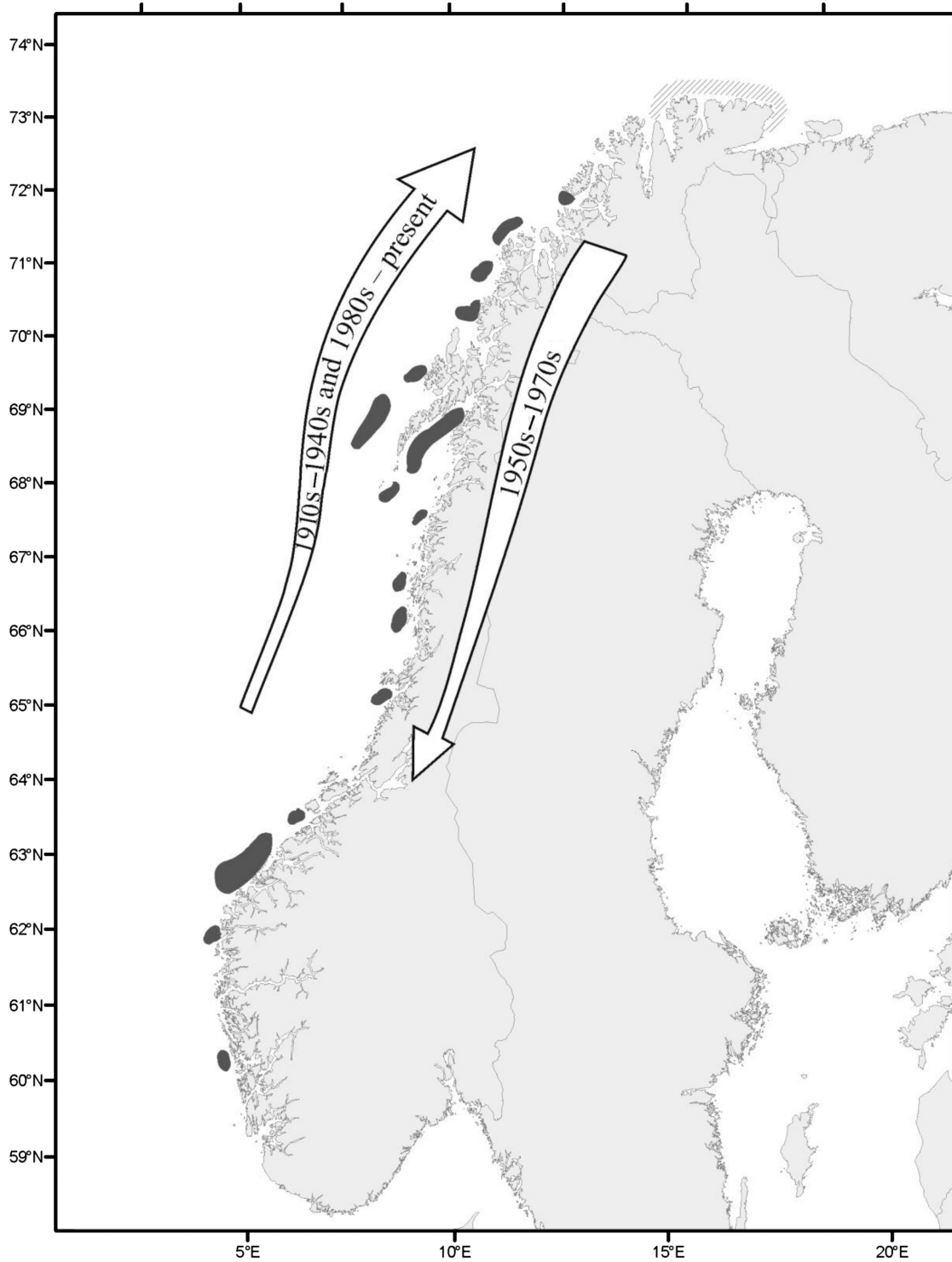


Figure 7. Displacement of Arcto-Norwegian cod spawning areas on a multidecadal time-scale. Shown is a northward displacement and increase in spawning-stock biomass during warmer periods, and a southward displacement and decrease in spawning-stock biomass during colder periods.

Limitation by the maximum possible distance of spawning migration

During the previous warming during the 1910s–1940s, many cod stocks in the North Atlantic, including the Arcto-Norwegian, moved north (Tåning, 1953; Drinkwater, 2006). During the

1930s, there are even observations of Arcto-Norwegian cod spawning as far north as the Bear Island region at 74°N in the western Barents Sea (Iversen, 1934). Because of the long spawning migration of Arcto-Norwegian cod, an expansion of its feeding habitats east and north in the Barents Sea during warm periods

might result in migration routes too far from the southernmost spawning areas, causing spawning to take place farther north along the coast. The resulting free pelagic drift of the offspring back into the Barents Sea would, in turn, result in settlement of young cod farther east and north in the Barents Sea where they would be able to survive owing to the higher temperature. Cianelli *et al.* (2007) demonstrated greater mortality of newly settled (0-group) cod attributable to cannibalism from older age groups in the southwestern part of the cod habitat in the Barents Sea. This mechanism could amplify the displacement of juveniles towards the northeastern Barents Sea during warm periods. A shift to a colder climate would result in higher winter mortality of 1- and 2-group cod, as shown by Ponomarenko (1984). This would be particularly important in the coldest portion of the Barents Sea, i.e. the northern and eastern parts, and would, in turn, lead to a more southwestern distribution of the entire stock, allowing for a more southerly spawning migration.

Inverse variations in size of subpopulations

The shift in spawning areas might be a response to inverse variations in two subpopulations of Arcto-Norwegian cod (Trout, 1956; Maslov, 1972), with separate feeding and spawning areas: (i) the western Barents Sea and Svalbard component spawning at the Møre spawning area, as indicated by Godø *et al.* (1984), and (ii) an eastern Barents Sea component spawning in Lofoten, Troms, and Finnmark. In cold periods, the transport of offspring towards the coast of Svalbard is relatively stronger than the transport with the eastern branch into the Barents Sea. This has been shown by Vikebø *et al.* (2007), who modelled growth and transport of cod larvae from the spawning area in Lofoten under a reduction of the Atlantic currents caused by a reduction in thermohaline circulation and a cooler climate. The cooler climate resulted in a greater reduction in the current branch into the Barents Sea than in the branch flowing along the west coast of Svalbard. Hence, more of the cod offspring would be transported to and settle on the west coast of Svalbard during cool periods. As the Svalbard component tends to use the Møre coast as its spawning area, this theory might explain the increased spawning intensity at Møre during cool periods. Conversely, in warm periods, more of the offspring will be directed into the Barents Sea, and the offspring fraction that happens to be transported along the west coast of Svalbard might, to a greater extent, be subjected to loss from the natural habitat of the continental shelf because of stronger currents that might transport larvae into the deep regions of the Fram Strait and Arctic Basin.

Influence of trophic interactions during pelagic drift of larvae and early juveniles

A third possible mechanism for the reduction in the western component and the southernmost spawning districts during warm periods could be predator–prey interrelationships, i.e. increased competition and/or predation during the early free-drifting pelagic stages. For example, herring (*Clupea harengus*) are a major predator on cod eggs (Melle, 1985), herring abundance has shown parallel fluctuations with the multidecadal climate fluctuations (Torensen and Østvedt, 2000), and a greater abundance of herring would result in relatively more predation on cod eggs in the Møre district than in the northern districts, because Møre is a major spawning area also for herring. A reduction in prey abundance for the adult stages during warm periods might also reduce the adult western stock component. For example, the abundant

Arctic prawn (*Pandalus borealis*) of the western Barents Sea and along the Svalbard coasts might be reduced in biomass in warm periods, and capelin (*Mallotus villosus*) might be displaced east into the Barents Sea (Gjøsæter, 1998).

Conclusions

It should be emphasized that the three mechanisms suggested above are not contradictory, and that a combination of any of them may cause the long-term shift in spawning areas. Fish stocks respond to climate variability and change in a multitude of ways, and the type of response depends on the periodicity of climate variations. The amplitudes of the interannual to decadal temperature variations are large in the Northeast Atlantic. At the Kola section of the Barents Sea, the decade-scale, peak-to-peak, mean annual sea temperature is 1.5°C. Phenomena such as individual growth rates (Jobling, 1981; Ottersen and Loeng, 2000), year-class formation (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989), and spatial distributions (Nakken and Raknes, 1987; Michalsen *et al.*, 1998; Ottersen *et al.*, 1998) have immediate responses to interannual temperature variations (Nakken, 2002). In other words, these rapid responses are linked to processes in population ecology, where there are relatively short links between temperature change and the ecological response. The multidecade-scale, peak-to-peak temperature signal is typically less than half the decade-scale signal, e.g. 0.7°C for the Kola section during the 20th century. This more moderate and long-term amplitude influences fish stocks in a different way, such as spawning migration and selection of spawning areas, as shown here.

Changes in spawning area seem to be linked to other kinds of ecosystem processes, e.g. changes in the life history of fish stocks, species interaction, trophic transfer, and evolutionary ecosystem processes. These are processes related to system ecology. Such processes will work on longer time-scales than those of population ecology, and the link between temperature change and its responses has a longer pathway. However, their implications on coastal societies could potentially be larger than inter-annual to decadal variations. In the study and assessment of climate change, it is important to be aware of these different types of response. The response described here in spatial change in spawning areas shows that it is linear and reversible within the observed magnitude of multidecadal climate variations (0.7°C). The temperature increase in the Barents Sea over the next 50 years attributable to global warming is predicted to be ~1.5°C (Furevik *et al.*, 2002). If the response in spawning behaviour is still linear, also within such a range of temperature variation, we would expect that the Arcto-Norwegian cod could migrate farther into the eastern and northern parts of the Barents Sea, and that the southernmost spawning districts might become even less important to the stock under future climate change.

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