



Thermal habitat for 0-group fish in the Barents Sea; how climate variability impacts their density, length, and geographic distribution

Elena Eriksen*, Randi Ingvaldsen, Jan Erik Stiansen, and Geir Odd Johansen

Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway

*Corresponding Author: tel: +47 55 235351; fax: +47 55 238687; e-mail: elena.eriksen@imr.no.

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Between 1980 and 2008, the climate changed from cold to warm conditions in the Barents Sea. Warmer conditions have been indicated as favourable for cod, haddock, and herring recruitment and unfavourable for capelin, although during recent years these relationships have weakened and need to be revised. Extensive survey observations of temperature and 0-group cod, haddock, herring, and capelin are explored, a bounded temperature range occupied by ~80–90% of 0-group fish (core thermal habitat, CTH) defined for each species, and an analysis made of how climate variability influenced density, length, and geographic distribution. Maximum fish densities were at 6.2°C for cod, 7.2°C for haddock, 7.0°C for herring, and 5.1°C for capelin. The area of CTH for cod, haddock, and herring increased from cold to warm years, as did the occupation area of each species. Capelin underwent a northeast distributional shift from cold to warm years. The 0-group fish were observed in a broad range of temperatures of –1 to 10.5°C. However, fish densities showed a dome-shaped distribution with temperature. Mean fish length was 7.1 cm for cod, 8.9 cm for haddock, 7.0 cm for herring, and 4.6 cm for capelin, with length distributions exhibiting a non-uniform response to temperature.

Keywords: 0-group, Barents Sea, capelin, climate change, cod, fish, haddock, herring, temperature.

Introduction

The Barents Sea fish community is dominated by a few large stocks, including Arctic cod (*Gadus morhua*), Barents Sea capelin (*Mallotus villosus*), Northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring-spawning herring (*Clupea harengus*), hereafter referred to as cod, capelin, haddock, and herring, respectively. Currently, these stocks are among the largest stocks of fish in the whole North Atlantic.

The stocks spawn along the Norwegian (capelin, cod, haddock, and herring) and Murman (capelin) coasts and offshore along the continental shelf (haddock) from February to April. Eggs and/or larvae are carried north and east by ocean currents. 0-group (5–7 months old) cod and capelin distribute widely in the Barents Sea. However, the densest concentrations of cod are found in a central area, and the densest concentrations of capelin in central and northern areas (Eriksen *et al.*, 2011; Eriksen and Prozorkevich, 2012). 0-group herring and haddock occupy smaller areas and are rarely found in the north. The densest concentrations of herring and haddock are found in central and coastal areas, although in some years greater densities

are present in the western (haddock) and eastern (herring) areas (Eriksen *et al.*, 2011; Eriksen and Prozorkevich, 2012).

The quality of eggs, and the subsequent survival of larvae, depends on the biomass and quality of the spawners' condition and age structure (Ponomarenko, 1973; Marshall *et al.*, 1998; Hysten *et al.*, 2008). The distribution and the survival of juvenile fish are also influenced by environmental factors, and warmer temperature conditions have been reported to be favourable for cod, haddock, and herring recruitment (Sætersdal and Loeng, 1987; Loeng and Gjørseter, 1990; Ottersen and Loeng, 2000).

Temperature influences metabolic processes and is, along with prey availability, the most important factor determining growth rates in fish (Brett, 1979). Loeng and Gjørseter (1990) studied the relationship between temperature and growth of 0-group fish in the Barents Sea and found positive relationships between temperature, growth, and the availability of food. In the areas with higher temperature and higher food concentration, the growth rate is higher (Suthers and Sundby, 1993). Temperature therefore influences the larvae and 0-group fish (fish 5–7 months old) directly through metabolism and indirectly through food availability.

Cod, haddock, herring, and capelin represent different biogeographic groups, so they may be differently influenced by climate variability. Stensholt and Nakken (2001) studied ambient temperature for 0-group fish and found that larger cod, haddock, and herring were associated with warmer water masses, whereas the opposite was found for capelin. Eriksen *et al.* (2011) studied 0-group fish biomass and abundance fluctuations during the period 1980–2009 and found that, after 1997, several successive strong year classes of capelin arose, haddock, and herring abundance increased, whereas no clear relationship between the recruitment of cod and temperature was found. These results warrant a new study of the relationship between climate and recruitment of these four fish stocks in the Barents Sea.

The Barents Sea climate varies on time-scales from a few years to several decades (Ingvaldsen and Loeng, 2009). There was a cold period in the late 1970s and early 1980s, and from then until now there has been a generally increasing trend in oceanic and atmospheric temperatures (Ingvaldsen *et al.*, 2003). The increase has been particularly strong in the past two decades, which has been the warmest on record (Levitus *et al.*, 2009; Boitsov *et al.*, 2012). During the past decade, warm water has spread farther north, increasing the area of the Barents Sea typified by warm Atlantic conditions and decreasing the area typified by cold Arctic conditions (Johannesen *et al.*, 2012).

During warmer periods, zooplankton biomass has been greater in the Norwegian and Barents Seas (Drobysheva, 1994; Dalpadado *et al.*, 2003; Orlova *et al.*, 2005). The advection of zooplankton, particularly *Calanus finmarchicus*, from the Norwegian Sea is important in enhancing zooplankton biomass in the Barents Sea (Skjoldal and Rey, 1989; Sundby, 2000), and high zooplankton biomass during warm years is presumably attributable to a greater inflow of advected organisms (Drobysheva, 1994; Dalpadado *et al.*, 2003; Orlova *et al.*, 2005).

In this paper, we use data from more than 8000 stations over a period of 30 years (1980–2008) from surveys in the Barents Sea during August/September to explore the following questions: what is the thermal habitat for 0-group fish (cod, haddock, herring, and capelin) in the Barents Sea, and how does climate variability influence their density, length, and spatial distribution?

Material and methods

The Barents Sea is a high-latitude, arctoboreal shallow shelf sea, and its circulation is dominated by the Norwegian Atlantic Current entering through the Bear Island Trough. Some of the Atlantic Water flows eastwards parallel to the coast towards Novaya Zemlya, and another part flows northeastwards and into the Hopen Deep (Figure 1). South of the Atlantic inflow, the Norwegian Coastal Current, flows along the northern Norwegian and Kola coasts.

The Atlantic and coastal inflows keep the southern part of the Barents Sea relatively warm. In the northern parts of the Barents Sea, cold Arctic Water flows southwest near the surface, keeping the northern part of the Barents Sea relatively cold. The border between the Arctic and Atlantic water masses is referred to as the Polar Front, which tends to be stationary and distinct in the west, but more variable in the east. Eriksen *et al.* (2011) defined the Barents Sea in several boxes, the box referred to as the “central area” containing the majority (ca. 70–80% for cod, haddock, and herring, and ca. 50% for capelin) of 0-group fish biomass. However, high biomasses were also observed in neighbouring boxes. In our study, we therefore modified that “central

area” of Eriksen *et al.* (2011) to include also the areas of these high biomasses, which we call the “core area” of 0-group fish (the box shown in Figure 1).

Survey

The international 0-group fish survey in the Barents Sea has been conducted annually during August/September since 1965. From 2003, the survey has been part of a joint Norwegian–Russian ecosystem survey, designed and carried out in cooperation between the Institute of Marine Research (IMR), Norway, and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia. 0-group fish were caught with pelagic trawls at three different depths down to 60 m (0–20, 20–40, 40–60 m). Further trawling details and procedures are given in Anon. (2004) and Eriksen and Prozorkevich (2012).

Biological data

Over the study period (1980–2008), 8879 stations were sampled for 0-group fish. Data are taken from the Joint Norwegian–Russian 0-group database, which underwent a complete revision and quality check in 2009 (Eriksen *et al.*, 2009). We therefore expected some of our results to differ from those based on the earlier version of the database. 0-group fish were identified by species, and body length was measured to a precision of 1 mm, then further aggregated into length groups of 0.5 cm.

Abiotic data

The temperature data are from CTD samples taken at each 0-group trawl station. The CTD profiles were taken either before or after trawling, and in this study, we used the temperatures aggregated to standard depths (5, 10, 20, 30, 40 m, etc.) to determine core temperature habitat and annual ambient temperature for the various fish species.

The temperature conditions influenced by inflow of Atlantic water were categorized by the annual mean temperature averaged from 50 to 200 m at the Fugløya–Bear Island section. The annual mean temperature from 1980 to 2008 was 5.5°C, with a minimum of 4.6°C and a maximum of 6.4°C (<http://www.imr.no/sjomil>), and years were categorized into average (long-term mean temperature $\pm 16\%$), cold (below average), and warm (above average; Figure 2).

Fish density and length

Fish density, as individuals per square nautical mile (nautical mile²), for each trawl haul was calculated from catch data and information on depth interval, effective opening, and distance trawled. The method is further described by Dingsør (2005) and Eriksen *et al.* (2009). The Barents Sea was divided into 40 × 40 nautical mile grid cells, and fish densities were categorized into four groups: no catch, low density (<16% below long term average), average density (long-term average density $\pm 16\%$), and high density (>16% above long term average).

The mean fish length at each station was calculated based on the number of fish per length group weighted by total fish number. There are some stations without length measurements in the data, so these were removed from the analyses. The number of stations with length measurements varied between species: cod lengths were measured at 3503 stations, haddock at 2443 stations, herring at 1764 stations, and capelin at 2051 stations.

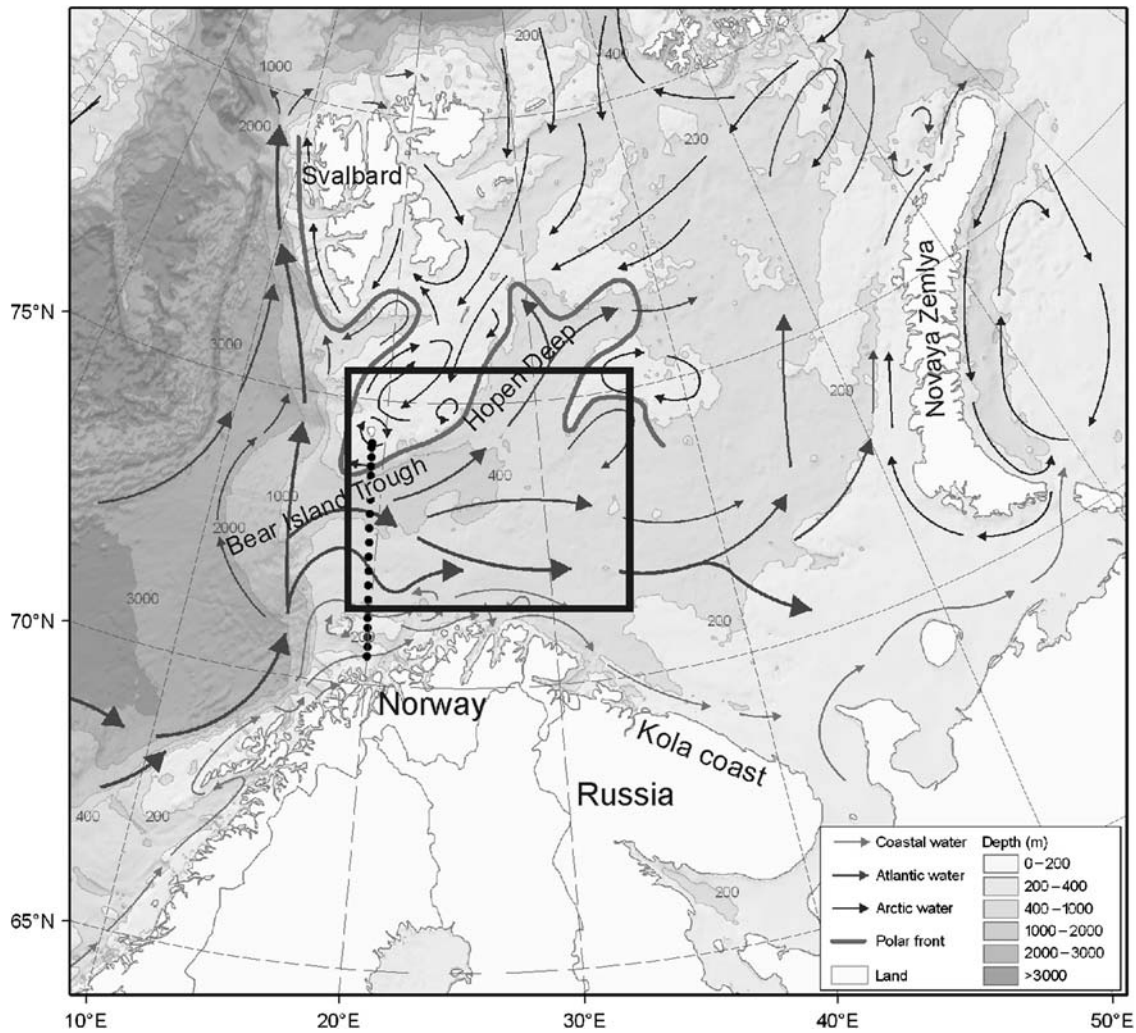


Figure 1. Overview of the Barents Sea geography and current system. The square indicates the core area for 0-group fish. The dotted line indicates the Fugløya–Bear Island section (FB).

Temperature

The mean temperature per station for the water layer 5–50 m was estimated as the average of the temperatures from standard depths. Temperature was measured at a total of 6115 CTD stations. As with fish density, temperature is presented by grid cell (40 × 40 nautical miles) in the maps (see below).

Ambient temperature was calculated using the mean temperature and the number of fish per station, weighted by total fish number, a method described by *Ottersen et al. (1998)* and *Stensholt and Nakken (2001)*.

Statistical modelling

We investigated the response of 0-group fish density and the length of cod, haddock, herring, and capelin to temperature. We used generalized additive models in the R (version 2.12.2) package *mgcv* (*Wood and Augustin, 2002*). The fish density (D_i) and fish length (L_i) of each species in sample i (i.e. station) were fitted to the covariate according to the following models:

$$D_i \text{ and } L_i = s(T) + \text{year}_i + e_i \quad (1)$$

$$D_i \text{ and } L_i = s(T) + \text{TempCond}_i + e_i, \quad (2)$$

where the predictors included the smoothed fits of the mean temperature at 0–50 m [$s(T)$] for sample i . The variable year was entered as a random variable [Equation (1)], and temperature condition (TempCond_{*i*}; see above how years were categorized into cold, average, and warm) was included as a factor in the model [Equation (2)]. The term e_i denotes the error for sample i . Transformation of the densities was needed because of skewed distributions. The best transformations, determined from data plotting, were found to be logarithmic.

The model, in which all terms included in the model were significant ($p \leq 0.001$), was checked by Akaike information criterion and genuine cross validation.

Core thermal habitat

A bounded temperature range was also estimated from the model as the temperature range within which modelled fish densities were larger than the mean modelled fish density (i.e. ~60% of the observations). This is associated with the temperature range occupied by ~80–90% of 0-group fish. This temperature range we hereafter refer to as core thermal habitat (CTH).

The upper and lower temperature limits of each CTH were used to define the spatial distribution, and total area, of the CTH by

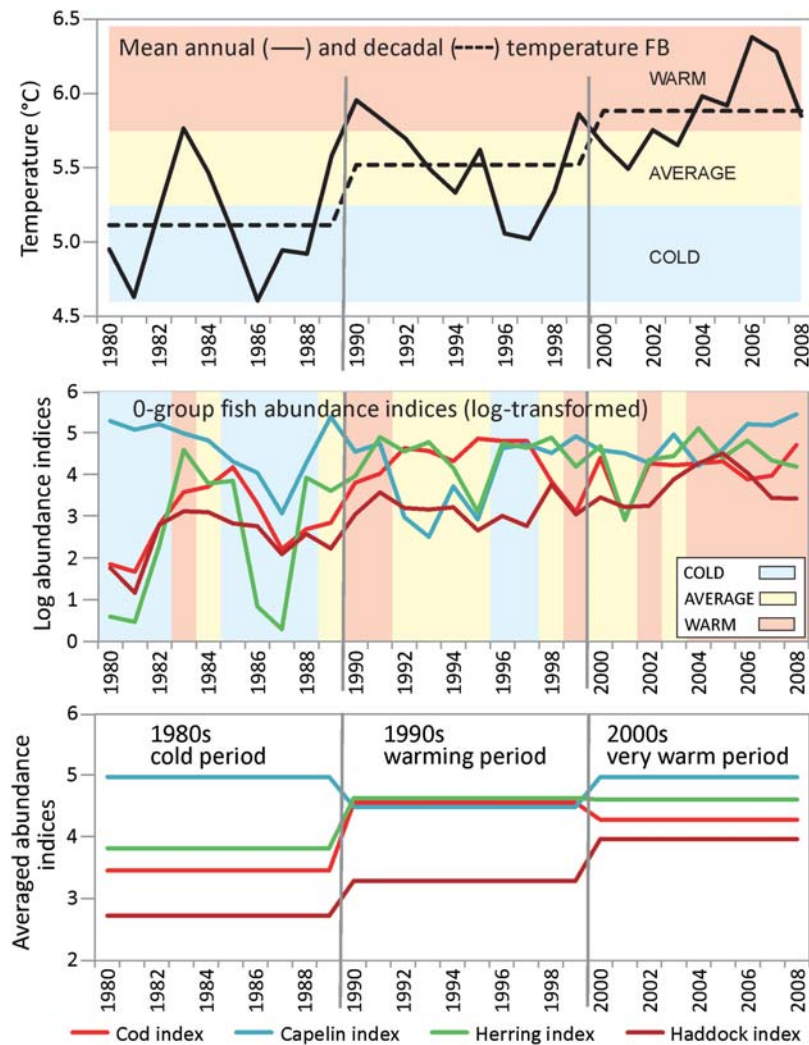


Figure 2. Variability in temperature at the Fugløya–Bear Island section and abundance indices by year and by decade for the period 1980–2008. Years/periods with different temperature conditions are shown in different colours.

identifying all 40×40 nautical mile grid cells with mean temperatures between the CTH temperature bounds.

Results

CTH and ambient temperature

Histograms of observed 0-group fish density and fish length by 0.5°C temperature interval, and the related additive models, are shown in Table 1 and Figure 3. The four 0-group fish species were observed in the temperature interval $-1^{\circ}\text{C} < T < 10.5^{\circ}\text{C}$ (Figure 3). However, the densities of all four species showed a dome-shaped distribution with temperature, with maximum densities at 6.2°C for cod, 7.2°C for haddock, 6.9°C for herring, and 4.9°C for capelin (Figure 3). The CTH, as defined above, was $4.4\text{--}8.0^{\circ}\text{C}$ for cod, $5.2\text{--}8.7^{\circ}\text{C}$ for herring, and $2.2\text{--}6.3^{\circ}\text{C}$ for capelin (Figure 3). For haddock, only the lower bound (5.3°C) was found. The highest temperature observed during the surveys was 10.5°C , so haddock CTH was defined as $5.3\text{--}10.5^{\circ}\text{C}$, based on these observations.

The ambient temperature for each stock varied between years and species (Table 2). The long-term mean ambient temperature was 6.0°C for cod, 6.6°C for haddock, 6.4°C for herring, and

5.0°C for capelin, close to the temperatures of maximum fish density (Figure 3). In general, the models reflected the observed distributions, although for the haddock model, the abundance at the highest temperatures was not well represented.

Fish density and length

The modelled and observed density distributions were skewed, at least for cod, herring, and haddock, with a stronger decline towards higher temperatures indicated by the asymmetrical distribution (Figure 3). The capelin distribution is more symmetrical.

When divided into cold, average, and warm years, the additive model maintained the dome-shaped distribution of densities (Figure 4). Also evident from these models is that the densities were lowest during cold years and highest in warm years, except those of cod which peaked in average years.

Mean fish length was 7.1 cm for cod, 8.9 cm for haddock, 7.0 cm for herring, and 4.6 cm for capelin (Table 2). The modelled and observed fish length distributions showed that the species did not have a uniform response to temperature (Figure 3). Haddock and herring length strongly increased with temperature up to $\sim 4\text{--}5^{\circ}\text{C}$, but at higher temperatures, the distribution patterns for fish

Table 1. Additive models for temperature associations of cod, haddock, herring, and capelin in the Barents Sea, with all terms included in the models being statistically significant (i.e. $p \geq 0.001$).

Model	s(MeanTemp)	F-value of s(MeanTemp)	F-value of s(years)	s(MeanTemp) and F-value			R ²	Genuine cross-validation score/scale
				Cold	Average	Warm		
Cod								
Density (1980–2008)	6.5	124.3	38.2	–	–	–	0.3 (25.8)	16.5 (16.4)
Fish length (1980–2008)	7.92	14.1	39.1	–	–	–	2.3 (26.0)	1.4 (1.3)
Density during years with different TempCond	–	–	–	6.8/16.9	6.6/50.8	8.3/56/9	1.5 (15.2)	18.7 (18.7)
Mean length during years with different TempCond	–	–	–	7.3/2.7	3.0/10.4	8.0/8.7	0.1 (12.8)	1.6 (1.6)
Haddock								
Density (1980–2008)	7.8	199.1	14.3	–	–	–	0.3 (25.9)	13.5 (13.5)
Fish length (1980–2008)	6.8	20.1	32.4	–	–	–	0.3 (31.5)	3.0 (3.0)
Density during years with different TempCond	–	–	–	4.7/32.7	7.6/63.7	6.7/113.6	0.2 (24.5)	13.7 (16.7)
Mean length during years with different TempCond	–	–	–	5.6/4.4	2.2/8.9	6.7/11.2	0.1 (12.3)	3.8 (3.8)
Herring								
Density (1980–2008)	7.7	107.9	20.3	–	–	–	0.2 (19.6)	16.2 (16.1)
Fish length (1980–2008)	3.7	63.7	26.9	–	–	–	0.4 (38.0)	1.6 (1.6)
Density during years with different TempCond	–	–	–	5.7/15.4	6.7/35.5	7.7/60.0	0.1 (14.5)	17.1 (17.1)
Mean length during years with different TempCond	–	–	–	1.0/25.7	1.8/24.1	3.6/38.7	0.2 (19.6)	16.2 (16.1)
Capelin								
Density (1980–2008)	5.5	108.4	50.9	–	–	–	0.2 (24.9)	20.3 (20.8)
Fish length (1980–2008)	4.7	71.0	12.6	–	–	–	0.2 (23.9)	0.8 (0.8)
Density during years with different TempCond	–	–	–	5.0/14.7	5.3/13.8	6.0/69.1	0.1 (12.3)	25.6 (23.5)
Mean length during years with different TempCond	–	–	–	5.1/23.3	4.4/22.9	1.8/86.7	0.1 (15.1)	0.9 (0.9)

length are not easily interpreted, although the increase seems to level off. Cod and capelin length distributions showed a dome-shaped response to temperature, with maximum lengths at ~ 5.5 – 7.5°C for cod and 3 – 3.5°C for capelin (Figure 3).

When divided into cold, average, and warm years, cod, haddock, and herring were ~ 0.5 – 1.5 cm smaller in cold years than in average or warm years (Figure 4). Capelin length showed no distinct response to the subdivision into cold, average, and warm years.

Spatial distribution and temporal variation in fish density and length

The areas of CTH for cod, haddock, and herring increased between cold and warm years, as did the occupied area of the species (the total area occupied shown in grey in Figure 5). However, although the areas of greatest density of these three species expanded (haddock and herring) or contracted (cod) between cold and warm years, it did not shift. In fact, the greatest densities of all the studied species in cold, average, and warm years were mostly within the “core area”. Hence, despite a varying temperature regime, cod, haddock, and herring remained in the “core area”, showing a relatively strong coupling to a specific area. Capelin, on the other hand, showed a northeastward distributional shift between cold and warm years (Figure 5), indicating weaker coupling to a specific area.

The CTH pattern differed over time (Figure 6). For haddock, the area was relatively large and stable, and the core area (the

area with highest concentration of 0-group fish) was situated in the middle of this stable temperature region. For cod and herring, the area with a stable CTH was much narrower, with a sharp edge on the cold-front side (which also corresponds to the polar front) and a larger area, but variable, on the warm-front side. The areas with high densities were partly in the stable region and partly on the warmer side of it. For capelin, the stable area was also much smaller than for haddock, with a more symmetrical variation pattern. However, in contrast to cod and herring, the high 0-group fish densities were in the stable CTH.

The spatial distribution of fish of different lengths varied among species. The longest 0-group cod and haddock were found in the central and western areas, herring in the central and coastal areas, and capelin in the eastern and northern areas. The fish length range was also widest in those areas.

Discussion

The Barents Sea is a crucial nursery area for many fish species. During the past three decades, temperature condition changed from cold during the 1980s, to moderate in the 1990s, then to warm during the past decade (2000s), and 0-group fish abundance showed species-specific trends associated with this warming (Figure 2). Warmer temperatures are favourable for cod, haddock, and herring recruitment (at the 0-group stage), based on data from the 1980s and 1990s (Sætersdal and Loeng, 1987; Loeng and Gjosæter, 1990; Ottersen and Loeng, 2000). However, Eriksen *et al.* (2011) found less covariation between cod,

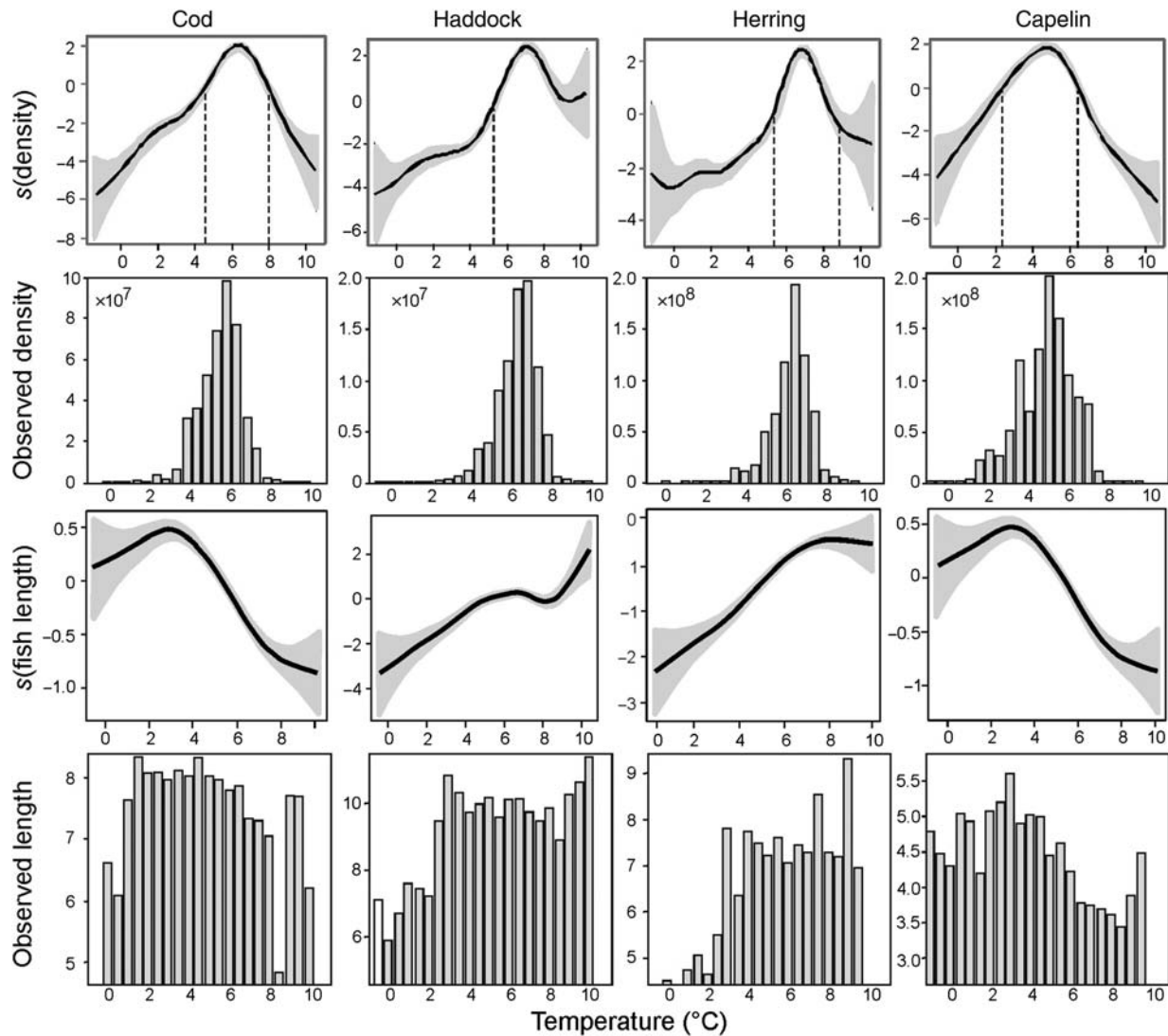


Figure 3. Estimated smoothing curves for fish densities, $s(\text{density})$, and fish length, $s(\text{fish length})$, and observed fish density (ind. nautical mile⁻²) and fish length (cm) by temperature for 0-group fish (cod, haddock, herring, and capelin). The solid line is the smoother and the shaded region indicates the 95% pointwise confidence interval.

haddock, and herring in the past 15 years. Therefore, it seems that during the past decade or so, some of the former “rules of thumb” (Figure 2) no longer apply.

The results show that cod, haddock, and herring were denser within the core area (Figure 5). In addition, 0-group fish in all length groups were found in that area, whereas they were more uniform in other areas. This demonstrates that the core area has better feeding conditions for all sizes of 0-group cod, haddock, and herring than the rest of the Barents Sea.

The core area is located at the entrance of Atlantic Water inflow to the Barents Sea. Bottom topography, including local banks and basins, governs the location of the currents in the area, and hence the distribution of water masses (Loeng, 1987). The high biomass of copepods (e.g. *C. finmarchicus*) observed during summer at the entrance to the Barents Sea (Orlova *et al.*, 2005) covers the whole core area. Most of the fish larvae reach or pass through the core area transported by ocean currents, and a consistent yearly inflow of relatively warm, plankton-rich water is the most likely

reason that this area is the main nursery area for 0-group fish in the Barents Sea.

All species studied had a CTH of 4–5°C, with maximum fish density at 6.2°C for cod, 7.2°C for haddock, 6.9°C for herring, and 4.9°C for capelin (Figure 3). For haddock, the areas with available CTH were large and stable over all years (Figure 6), showing that haddock has a large potential area in terms of temperature. Therefore, the observed variation in spatial distribution of this species is not governed by local temperature variation. For cod, herring, and capelin, the area with available CTH varied extensively year-on-year (Figure 6), supporting our notion that variability in fish density is linked to temperature variation.

In the northern part of the core area (Figure 5), high densities of cod, haddock, and herring are restricted by colder water (Figures 5 and 6). The northern bound of the CTH for these species corresponds to the Polar Front, which in this area has a stable position owing to the topography. Waters north of the front have different plankton communities than the core area

Table 2. Ambient temperature (°C) and mean fish length (cm) of 0-group cod, haddock, herring, and capelin, 1980–2008, under different temperature conditions (cold, average, and warm).

Year and parameter	Ambient temperature (°C)				Mean fish length (cm)			
	Cod	Haddock	Herring	Capelin	Cod	Haddock	Herring	Capelin
1980	5.6	6.1	5.5	5.5	5.7	7.0	5.1	3.7
1981	5.9	8.7	5.7	5.7	5.8	6.6	5.8	3.7
1982	4.4	5.5	4.8	4.2	6.3	7.4	5.7	4.2
1983	5.8	7.1	6.2	6.2	7.7	8.8	7.9	4.5
1984	6.1	7.5	5.9	6.1	7.3	8.4	9.4	5.0
1985	6.2	6.7	7.3	5.2	7.3	8.4	8.4	5.0
1986	6.0	6.7	6.1	5.9	6.3	7.2	5.7	3.8
1987	5.8	6.1	5.9	5.1	5.4	5.8	4.8	4.3
1988	6.3	6.4	6.7	4.5	6.5	7.6	6.7	4.5
1989	6.9	6.5	6.1	6.0	7.8	8.2	7.7	4.3
1990	7.0	7.8	6.9	5.2	8.3	9.9	9.2	4.6
1991	5.6	6.7	6.2	5.0	8.0	8.3	8.1	5.1
1992	5.7	6.6	6.3	5.2	8.0	9.4	8.9	5.8
1993	5.4	6.7	6.0	4.0	8.3	10.1	7.4	5.3
1994	6.1	6.4	6.4	4.3	8.7	9.9	6.6	5.9
1995	5.8	5.9	5.7	4.9	8.9	10.1	6.3	4.4
1996	5.6	6.4	7.1	4.1	7.7	10.3	6.2	5.0
1997	6.2	6.1	6.6	5.4	7.1	8.7	6.2	4.2
1998	6.0	5.7	6.3	5.1	8.2	10.5	7.0	4.4
1999	6.5	6.8	6.5	4.3	8.8	10.4	9.1	4.4
2000	6.4	6.5	6.5	5.9	7.4	8.1	6.3	4.0
2001	5.3	5.1	6.5	4.0	6.9	10.0	5.9	5.3
2002	4.8	6.0	6.3	4.6	7.7	10.7	7.7	4.3
2003	6.1	6.1	6.5	3.8	6.8	8.1	7.6	4.0
2004	5.7	6.6	6.9	4.8	8.4	11.1	7.7	4.7
2005	6.6	6.6	6.9	5.2	8.6	9.6	7.4	4.5
2006	6.5	7.4	6.4	5.1	8.9	10.2	7.7	4.9
2007	7.4	7.7	7.3	4.4	7.2	9.4	7.0	4.9
2008	6.8	6.6	7.4	5.7	7.2	8.7	5.7	4.2
Long-term mean (cm)	6.0	6.6	6.4	5.0	7.5	8.9	7.1	4.6
Cold years (cm)	5.8	6.2	6.5	5.1	5.4	7.7	6.1	4.3
Average years (cm)	6.0	6.2	6.3	4.9	7.8	7.8	7.3	4.8
Warm years (cm)	6.2	6.7	6.8	4.9	8.0	8.0	7.7	4.6

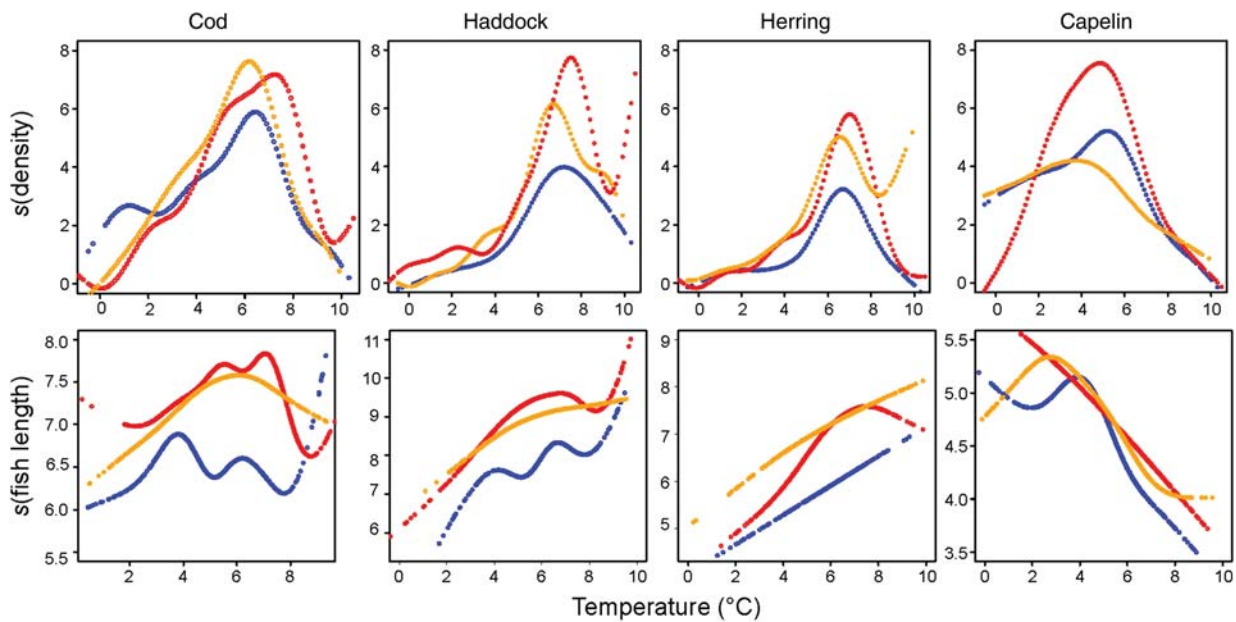


Figure 4. Estimated smoothing curves for fish density and fish length during years of different temperature. The blue line is for cold years, yellow for average years, and red for warm years.

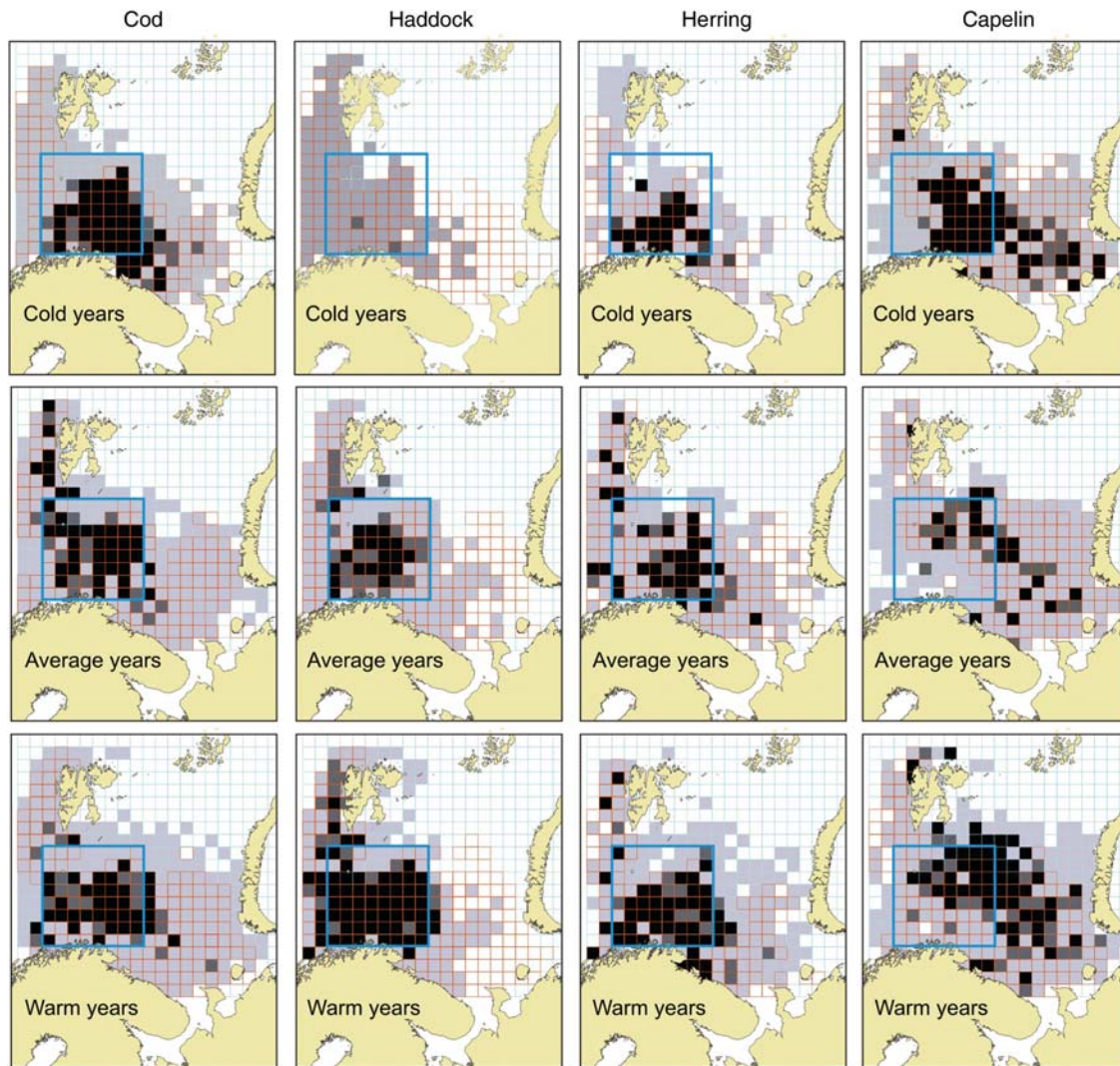


Figure 5. Spatial distribution of fish densities (light grey: below average; dark grey: average; black: above average) and CTH (red grid cells) for 0-group fish (cod, haddock, herring, and capelin) during the three decades 1980–2008. Fish density is shown during cold (top row), average (middle row), and warm (bottom row) years. The squares indicate the core area for 0-group fish.

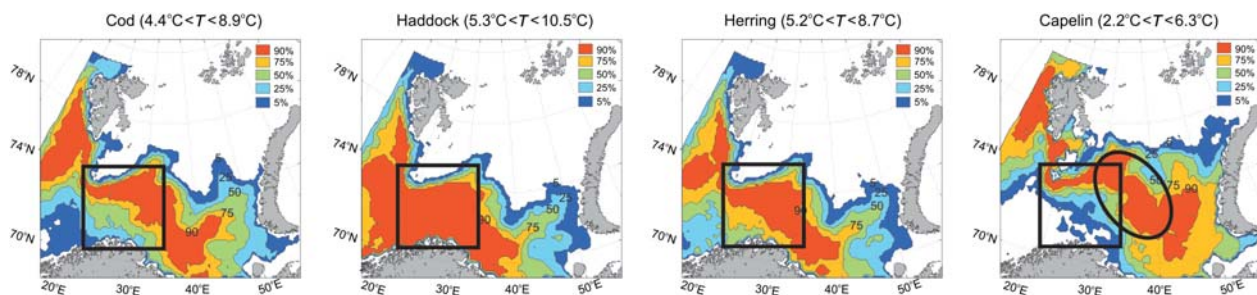


Figure 6. Variations in the distribution of waters having temperatures within the CTH for cod, haddock, herring, and capelin. Contoured values are the number of years (as a percentage of the total number of years; $n = 29$) when the water in each grid cell is within the temperature interval. The squares indicate the core area for 0-group fish, and the ellipse roughly shows areas of high capelin density taken from Figure 5.

for 0-group fish, which is dominated by Atlantic plankton species at high density (Drobysheva, 1994; Orlova *et al.*, 2005). Therefore, the northern distribution of high density areas of cod and herring

is restricted by a combination of oceanographic factors and food resources. Haddock showed average, but not high, densities also north and northeast of its CTH. This may be explained by

preferences for prey composition, density, and circulation processes (Werner *et al.*, 1996; Pedersen and Fossheim, 2006; Dalpadado *et al.*, 2009).

The southern warm boundary of each species' CTH varied considerably between years, except for haddock (Figure 6). Our results also showed an asymmetrical distribution of density with a stronger decline towards higher temperature (Figure 3). This asymmetry may point towards possible abrupt changes in the high-density areas of fish at high temperature. A similar relationship with temperature has been found for the scope for growth (i.e. the difference between the consumption needed for tissue maintenance and maximum consumption; Peck *et al.*, 2003). This also may be linked to a bioenergetic limit for distribution, as discussed in Pörtner and Peck (2011). For 0-group fish in the Barents Sea, this means that any further increase in temperature within the core area (Figure 5) may be suboptimal with respect to growth and survival.

Cod density and length were greatest in the temperature range 4.4–8.0°C, indicating that an increase in temperature may not lead to further increases in cod density and fish length (Figure 3). Similarly, Rogers *et al.* (2011) showed that increased summer temperatures in the coastal Skagerrak limit the growth of juvenile cod. Although cod spawning stock biomass was high, no abundant year classes of cod were formed during extreme warm years (2006–2007) in the Barents Sea, whereas several strong year classes were formed during moderate warm years (since 2008). This supports our results and earlier findings (Dingsør *et al.*, 2007; Eriksen *et al.*, 2011) that temperature may have an asymptotic effect on cod abundance. Hence, an increase in temperatures above 6.2°C (Table 2, Figure 4) may yield no further gain in 0-group cod abundance.

Our results showed that the highest densities of capelin were observed within the core area only during cold years (Figure 5), but that they shifted towards the northeast in warm years. In this respect, our results agree with those of Stensholt and Nakken (2001), who stated that larger 0-group capelin preferred colder waters than the other three species. The lower bound of the CTH was 2.2°C for capelin, and lower densities were found down to –1°C. Capelin are clearly, therefore, not restricted by the Polar Front, but more connected to mixed water masses, i.e. water of temperature between 0 and 3°C. During the past decade (2000–2009), there has been a substantial increase in areas with mixed water in the Barents Sea, whereas the increase in areas with Atlantic Water (temperature >3°C) has been less pronounced (Johannesen *et al.*, 2012). Such redistribution of water masses seems to affect capelin distribution and density more than the 0-group of other species.

Strong year classes of herring may negatively affect the survival of capelin larvae (Marti, 1956; Hamre, 1994; Gjøsaeter and Bogstad, 1998; Hallfredsson and Pedersen, 2007, 2009). However, the shift in the area occupied by capelin may have caused a considerable decrease in that species' overlap with young herring. In recent years (2007–2010), several strong year classes of capelin have arisen, despite the warm conditions. There might be a combination of several factors such as (i) high capelin spawning-stock biomass, (ii) low abundance of, and spatial overlap with, young herring, (iii) stronger inflow leading to a redistribution of Atlantic water masses and to drift of capelin larvae farther north, and (iv) a northeastward shift of the area occupied by capelin within the CTH.

The spatial distribution of length varied among species. The length and the size range of 0-group cod, haddock, and herring were largest in the core area (Figure 5), but for capelin, the

peaks were outside the core area in the northeast. Mean fish length was lowest in cold years for all species of fish studied (Table 2). There was not a uniform response to temperature (Figure 3): for haddock and herring, the length increased strongly with temperature up to ~4–5°C, whereas for cod and capelin, length showed a dome-shaped response to temperature, with maximum length at ~5.5–7.5°C for cod and 3–3.5°C for capelin. This means that a further increase in temperature will not lead to further increases in cod and capelin length (Figure 3), probably due to there being bioenergetic limits to fish growth. Additionally, fish length is not only affected by temperature in August/September, but also by spawner condition, spawning time and placement, access to food, and the temperature during the growing period.

Our results have shown abrupt changes in fish density with increasing temperature. Future climate change implies general warming of the Barents Sea, which further implies that the CTH for the four species studied here will move farther northeast into the Barents Sea. The spatial effect of temperature alone will therefore depend on whether the species are coupled to a specific geographic area (such as cod and herring) or are able to “follow” any redistribution of thermal habitat (such as capelin). Fish recruitment in the Barents Sea is a complex issue because it depends on a combination of many factors, both physical and biological (some of which are discussed above). Hence, more research is required before any clear conclusions on future trajectories of fish stock parameters can be drawn.

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