



Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions

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Long time-series of data from the Barents Sea (BS) are analysed to contrast the climate, fishing pressure, plankton, pelagic fish, demersal fish, and interactions between trophic levels in a recent decade (2000–2009) with the period 1970–1999. During the past four decades, fishing pressure and climatic conditions have varied greatly in the BS, and stock levels have fluctuated substantially. Trophic control has changed from mainly bottom–up to top–down, then back to mainly bottom–up. No clear evidence for persistent ecological regimes was found. The past decade has been the warmest on record, with large stocks of demersal and pelagic fish, and increasing abundances of krill and shrimp. Except perhaps for the rather less-studied Arctic species, the short-term effect of the recent warming has been positive for BS stocks. However, as many of the long-established relationships and mechanisms in the BS seem to be changing, the long-term effects of warming are uncertain.

Keywords: Barents Sea, ecosystem state, time-series, trophic regulation.

Introduction

Removing top predators such as demersal fish through fisheries might cause trophic cascades and abrupt changes in ecosystem state (Frank *et al.*, 2005). The trophic cascades in turn set the stage for ecological feedback loops (hysteresis) arresting the alternative state, despite the reversal of the external forcing factors (discontinuous regime shifts; Collie *et al.*, 2004). Such discontinuous regime shifts and the associated hysteresis might explain the lack of recovery of demersal stocks despite improved climate conditions and decreased fishing pressures in North Atlantic shelf seas such as the Baltic Sea, North Sea (NS), and eastern Scotian Shelf (ESS; e.g. Choi *et al.*, 2005; Casini *et al.*, 2009; Fauchald, 2010; Lindegren *et al.*, 2011). Despite a high level of exploitation of demersal fish, no such dramatic shifts have been reported from the Barents Sea (BS), which currently holds the largest cod stock in the world, with a stock level comparable with the 1950s (ICES, 2010a). The potential for trophic cascades and discontinuous regime shifts varies with the idiosyncrasy of the ecosystem. In general, warmer, more-species-rich ecosystems and periods tend to be more robust to the fishery-induced changes in trophic control (from bottom–up to top–down), potentially

leading to trophic cascades (Frank *et al.*, 2006, 2007; Petrie *et al.*, 2009).

In the BS, there is a strong influence of Atlantic water mass that meets and mixes with Arctic water masses along the Polar Front (Loeng, 1991). Because of the Atlantic inflow, the BS is warm compared with other areas at the same latitude, but the oceanographic conditions are highly variable. The BS fauna consists of both Atlantic and Arctic species (Ekman, 1967) and is therefore relatively diverse compared with other shelf seas at similar latitudes (e.g. the Kara Sea; Essipov, 1952). Trophic control in the BS has been proposed to be of a wasp–waist form, i.e. controlled by intermediate trophic levels, because the dominant pelagic fish, the capelin (*Mallotus villosus*), has a top–down effect on its prey, and a bottom–up effect on its predators (Ciannelli *et al.*, 2006; Yaragina and Dolgov, 2009). The top–down effects that capelin has on its prey are inferred from reductions in biomass and changes in the size structure of zooplankton at high-abundance levels of capelin, whereas the bottom–up effect is inferred from reduced cod growth and fecundity, breeding failures of seabirds, and starvation and migration of seals at low capelin abundance levels (reviewed in Gjøsæter *et al.*, 2009).

Ecological regime shifts were defined in Lees *et al.* (2006) as rapid (2–5 years), high-amplitude, low-frequency (minimum duration of 10 years) changes affecting at least three trophic levels. Ecosystem assessments in the Baltic Sea, NS, and ESS show that in those ecosystems, changes are consistent with such ecological regime shifts (Choi *et al.*, 2005; Möllmann *et al.*, 2008; Kenny *et al.*, 2009).

According to Lees *et al.* (2006), the BS experienced a regime shift in the late 1960s associated with the collapse in the Norwegian spring-spawning herring (*Clupea harengus*) stock. Since the late 1960s, both temperature and the abundance of species at several trophic levels have fluctuated in the BS, and so has the fishing pressure. In particular, there has been a warming trend, and the past decade in the BS has been the warmest ever on record (Levitus *et al.*, 2009). However, temporal variation in trophic regulation and ecological regime shifts has not been studied for the full period from 1970 until the present. In this recent warm decade, the capelin stock collapsed, but no negative effects were observed in the top predator community (Gjøsæter *et al.*, 2009), suggesting that key trophic interactions and the trophic control in this system are changing.

In this paper, we examine changes in climate, fishing pressure, stock fluctuations, trophic control, and ecosystem state in the BS from 1970 to 2009, with emphasis on the recent decade. We attempt to answer the questions: (i) has the trophic control changed over time and (ii) is there evidence of ecological regime shifts in the period from 1970 to 2009? Finally, we discuss the evidence for effects of the recent warming on the BS ecosystem.

Material and methods

Study area

The BS is a high-latitude shelf sea of 1.6 million km² (Carmack *et al.*, 2006) with a mean depth of 230 m. It is bordered by the northern Norwegian and Russian coasts, and the Novaya Zemlya Islands. The 500-m depth contour is used to delimit the BS towards the Greenland Sea, Norwegian Sea, and the polar basins (Figure 1). Novaya Zemlya separates the BS and the Kara Sea.

The ocean circulation is dominated by the Norwegian Atlantic Current bringing warm, saline Atlantic water into the area from the south. Atlantic water extends over the western and central parts of the ocean, whereas cold, fresher Arctic water dominates in the northern part. The borderline between the two main water masses is called the Polar Front, which is fairly sharp in the western parts of the BS. Smaller branches of subducted Atlantic water enter the Arctic areas both below the front and from the north around Svalbard (Loeng, 1991). In the eastern BS, the Polar Front is variable and tends to be strong in cold years and weak in warm years.

The northern BS is seasonally ice covered, and in winter the ice edge usually follows the oceanic fronts. The ice edge is normally in its northernmost position in September, when only the remote northern parts are ice covered (Figure 1). The seasonal ice melt stabilizes the upper layers and is associated with a “spring” plankton bloom following the receding ice edge (Sakshaug and Skjoldal, 1989).

The biotic part of the BS ecosystem consists of a mixture of Arctic and Atlantic (boreal) species (Ekman, 1967). The mesozooplankton fraction is dominated by *Calanus* copepods, with *Calanus finmarchicus* dominating in Atlantic water and *C. glacialis*

in Arctic water. The larval stages of *C. finmarchicus* are the principal food of fish larvae, and important for the variability in the recruitment of herring, cod, and haddock (Dalpadado *et al.*, 2009). Capelin larvae, on the other hand, are suggested to forage on small prey organisms frequently found among the coastal zooplankton and are therefore less dependent on the recruiting generation of *C. finmarchicus* (Fossheim *et al.*, 2006).

Krill is another important plankton group in the BS. *Thysanoessa inermis*, regarded as a shelf species, is found throughout most of the Atlantic part of the BS, being particularly abundant south and east of Svalbard. The areas of high abundance of *T. inermis* overlap with concentrations of capelin, and this species can constitute up to 60% of the diet of adult capelin (Dalpadado and Mowbray, in press). *Thysanoessa raschii* is a cold-water species and is mostly limited to shallow, less-saline waters in the east (Zhukova *et al.*, 2009). The largest of the krill species, *Meganyctiphanes norvegica*, is usually restricted to slope areas of the Norwegian Sea, but penetrates to some extent the BS along its deeper trenches. Pelagic amphipods are important, particularly in the colder parts. The larger amphipod species *Themisto libellula*, which is found in huge concentrations in Arctic water, is an important prey of cod, polar cod (*Boreogadus saida*), and mammals associated with the ice edge, whereas the smaller *T. abyssorum* is an important component of the foodweb in Atlantic/boreal waters.

More than 3000 benthic species and 200 fish species have been recorded in the BS. The northern shrimp (*Pandalus borealis*) is probably the most abundant benthic-pelagic invertebrate. The polar cod, a true Arctic species, capelin, and juvenile herring are the most abundant pelagic fish. Blue whiting (*Micromesistius poutassou*) are found in the deeper areas of the BS when the stock size in the Norwegian Sea is large (Heino *et al.*, 2008). Other pelagic fish are rarer. Cod dominate the biomass of demersal fish, but the area also sustains a large population of haddock (*Melanogrammus aeglefinus*). In addition, the BS has some of the largest concentrations of seabirds in the world and a rich fauna of sea mammals (Stiansen *et al.*, 2009).

The interactions between capelin, cod, and herring are considered to be key processes in the BS (Hamre, 1994; Ushakov and Prozorkevich, 2002). Strong year classes of herring are associated with recruitment failure and stock collapse of capelin, most likely caused by herring predation on larvae (Gjøsæter and Bogstad, 1998; Hallfredsson and Pedersen, 2009). In turn, capelin abundance influences the condition of its main predator, cod, as well as other predators (Gjøsæter *et al.*, 2009), and the abundance and size distribution of its zooplankton prey (Dalpadado and Skjoldal, 1991; Dalpadado *et al.*, 2002).

The BS has been harvested for centuries. Whaling ended with the depletion of the large baleen whale stocks at the start of the 1900s. In recent decades, under strict regulations, minke whales and harp seals have been harvested by Norway and Russia. Until the introduction of the quota system combined with exclusive economic zones in the mid-1970s, the overall fishing pressure increased, resulting from technological developments in fishing. As a consequence, the Norwegian spring-spawning herring collapsed in the late 1960s (Nakken, 1998). There was a fishery on polar cod in the 1970s, but the fishery has been negligible since then. The main current fishery is on cod, haddock, and capelin, with a less and more variable fishery on shrimp and a few other demersal fish.

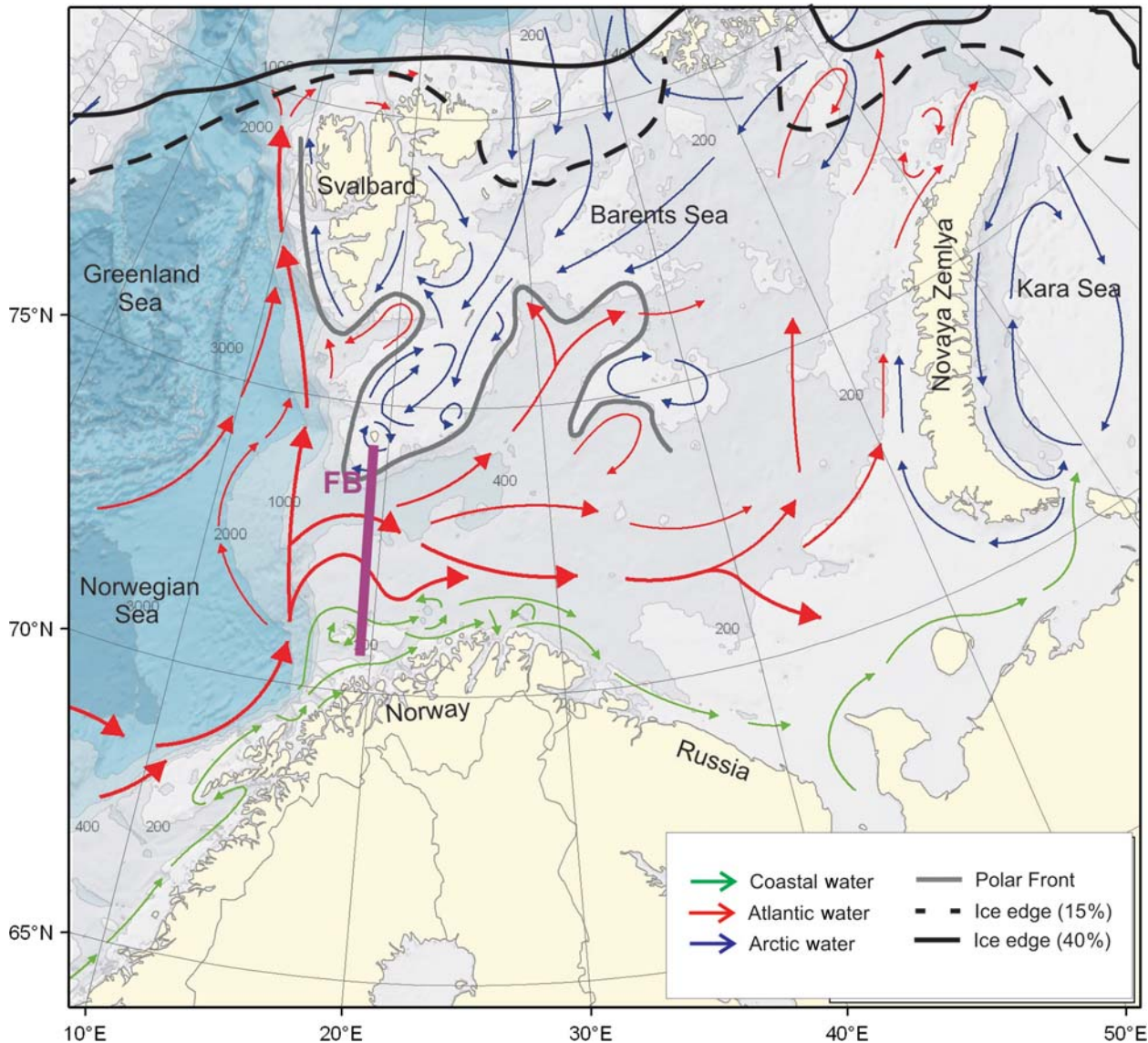


Figure 1. The main circulation and water masses in the BS. The mean ice edge, using 15% (solid) and 40% (dashed) ice concentration, in September (black), the Polar Front (grey), and the FB section (purple).

Monitoring data

The most extensive and longest time-series on oceanography and living resources in the BS are collected on standard sections and area surveys run by the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia and the Institute of Marine Research (IMR), Norway. The Fugløy-Bear Island (FB) section is a standard section in the BS and is located across its western entrance (Figure 1). Annual hydrographic monitoring of the section started in 1964, and since 1977, it has been sampled up to six times annually.

There are three annual area surveys in the BS. The Joint IMR–PINRO winter survey for demersal fish, started by IMR in 1981, is conducted annually in February/March. It covers the southern ice-free part, and its main target species are cod and haddock. In addition, PINRO runs a demersal survey in November/December. The ecosystem survey is conducted jointly by IMR and PINRO between August and early October. The ecosystem survey started in 2004 as a combined effort including several

other ongoing surveys, the most important being the acoustic survey for pelagic fish and the international 0-group survey, which date back to 1972 and 1965, respectively. As part of these surveys, oceanographic measurements have been taken. The ecosystem survey and its predecessors were conducted in the period of least ice cover and is the only survey covering also the Arctic part of the BS.

Commercial catch statistics from all countries as well as survey data are reported to ICES. The assessment of the historical development of the stocks and short-term prognosis are conducted by ICES assessment working groups, the most important for the BS being the Arctic Fisheries Working Group (AFWG).

Time-series of data

Available time-series are provided in Supplementary Table S1 and represented as colour matrix anomalies (Supplementary Figure S1), with references and explanations (Supplementary Tables S2 and S3). Below, we describe the time-series in more detail. As

Table 1. List of variables with units included in the multivariate analyses for the periods 1970–2009 and 1986–2009.

1970–2009	1986–2009	Variable	Unit
Yes	Yes	Russian krill index	ind. m ⁻³
Yes	Yes	Capelin mean weight at age 2	g
Yes	Yes	Capelin stock biomass (age 1+)	Million tonnes
Yes	Yes	Herring stock biomass (ages 1 and 2)	Million tonnes
Yes	Yes	Cod stock biomass (age 3+)	Thousand tonnes
Yes	Yes	Haddock stock biomass (age 3+)	Thousand tonnes
Yes	Yes	Cod mean weight at age 5	kg
Yes	Yes	Shrimp stock	No unit (biomass/biomass MSY)
	Yes	Krill biomass 0-group hauls	g m ⁻²
	Yes	Mesozooplankton	g m ⁻² dry weight
	Yes	0-group capelin abundance	Million individuals
	Yes	0-group herring abundance	Million individuals
	Yes	0-group polar cod abundance	Million individuals
	Yes	Polar cod mean weight at age 2	g
	Yes	Polar cod stock biomass (age 1+)	Million tonnes
	Yes	0-group redfish abundance	Million individuals
	Yes	0-group long rough dab	Million individuals
	Yes	0-group cod abundance	Million individuals
	Yes	0-group haddock abundance	Million individuals
	Yes	Haddock mean weight at age 5	kg

There are more variables for the period 1986–2009 owing to the onset of new surveys and investigations in the 1980s. See also the Supplementary material. Weights are wet weight unless otherwise stated.

the series vary in length, the multivariate analyses (see below) were performed on two sets of biotic data, one starting in 1970 and one in 1986 (Table 1, see also Supplementary Table S1). We only included time-series without missing data, except the capelin data (averages from 1972 to 1975 were used for 1970 and 1971).

Climate

We included indices representing the atmospheric influences, ice coverage, and sea temperature. The winter (December–March) North Atlantic Oscillation (NAO) index was used as a measure of the atmospheric influence (downloaded from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>).

The summer open water index (SOWI) is a quantitative area-based measure of the variation in the ice-free area north of 79°N integrated over summer. A high value corresponds to a large fraction of open water and an index equal to zero means that the ice edge is south of 79°N throughout summer. Because the BS always (at least to date) is ice covered north of 79°N in winter, this index is an indicator of the area experiencing seasonal ice melt.

Temperature of Atlantic water in the BS is measured at the standard section FB (Figure 1). The area of Atlantic water ($T > 3^{\circ}\text{C}$), Arctic water ($T < 0^{\circ}\text{C}$), and mixed water ($0^{\circ}\text{C} < T < 3^{\circ}\text{C}$) was calculated based on the mean 50–200 temperature fields from temperature measurements taken during the annual scientific surveys in the third quarter. To ensure complete data coverage each year, the area calculations were restricted to the area 72–80°N 20–50°E.

Zooplankton

Time-series data on mesozooplankton biomass, but not on species composition, are available from the early 1980s. The zooplankton samples are obtained with a 56-cm diameter WP2 plankton net of 18- μm mesh. The WP2 net catches best represent the mesozooplankton fraction dominated by copepods. A Russian krill time-series starting in the 1950s is now taken as a part of the Russian demersal survey in November/December (Anon., 1983, 1996,

2000; Zhukova *et al.*, 2009) and was also used in our analysis. A time-series on krill based on the 0-group survey data are available from 1980.

Fish recruitment

The 0-group survey has used a standard trawling procedure since 1980 consisting of pelagic trawling (Harstad trawl with 20 × 20 m mouth opening), at three or more depths. The 0-group abundances of cod, haddock, redfish (*Sebastes* spp., mostly *S. mentella*), long rough dab, polar cod, herring, and capelin are estimated yearly using a stratified sample mean method of swept-area estimation.

Pelagic fish biomass and weights

Data on capelin and polar cod stock biomass (age 1+) and mean weight at age 2 were obtained during the acoustic survey for pelagic fish and the ecosystem survey. Polar cod data only date back to 1986.

Biomass of juvenile herring (ages 1 and 2) was calculated from the number of individuals estimated from virtual population analysis and taken from the most recent herring assessment (ICES, 2010b) and standard weights at age (9 and 20 g). This is the same approach as taken by Gjosæter and Bogstad (1998). Blue whiting are found in the deeper southwestern parts of the BS in some years. An acoustic estimate of blue whiting has been calculated from the ecosystem survey data since 2004.

Demersal fish biomass and weights

Time-series on cod and haddock biomass (3+) and mean weight at age 5 from the stock assessment (VPA) made by AFWG (ICES, 2010a) were used. Weight-at-age data for cod and haddock are available from 1946 and 1980, respectively. In addition to cod and haddock, assessments of Greenland halibut and deep-water redfish are made by ICES. The assessment on deep-water redfish was last updated in 2003 and the assessment of Greenland halibut in 2006.

Other ecosystem components

A dedicated shrimp survey was conducted from 1981 to 2004. Shrimp are now sampled with a demersal trawl (a Campelen 1800) together with other benthic fish and invertebrates as part of the ecosystem survey. Shrimp stock assessment data provided by the NAFO/ICES *Pandalus* working group (NIPAG) were used here.

Fishing

Landing data for different species are among the longest time-series available. Fishing mortalities (F) are provided by AFWG on species with VPA assessments. We included average fishing mortalities for ages 5–10 for cod and 4–7 for haddock. For capelin, relative fishing mortality was calculated as the sum of catches in autumn and the next spring divided by biomass in autumn. Relative fishing mortalities of shrimp were taken from the latest shrimp stock assessment.

Analysis

As a measure of trophic control, we used correlations between functional groups/trophic levels (biomass of demersal fish vs. pelagic fish, demersal fish vs. shrimp, pelagic fish vs. zooplankton) following Frank *et al.* (2006) and Petrie *et al.* (2009). Negative correlations imply top–down control, whereas positive correlations imply bottom–up control. Centred 15 years sliding window correlations (Frank *et al.*, 2006) and correlation coefficients by decade were calculated to investigate changes in trophic control over time.

To detect abrupt temporal shifts in species composition associated with succession (Legendre *et al.*, 1985) and ecological regime shifts, chronological clustering can be used following DeYoung *et al.* (2004) and ICES (2011). The R package “mvpart” was used to perform chronological clustering, as described in Borcard *et al.* (2011), to cluster the years from 1970 to 2009 into periods according to the changes in the biotic time-series. The procedure uses cross-validation to find the number of clusters that minimized the cross-validation relative error.

As a measure of ecosystem state, principal components analysis (PCA) was used to integrate information across multiple time-series comprising different trophic levels and other aspects of the ecosystem (Kenny *et al.*, 2009; ICES, 2011). The time-trajectories of the first principal components were then used to evaluate the temporal development in ecosystem state (e.g. Kenny *et al.*, 2009). The analysis was done with the R package “vegan” (Oksanen, 2011).

Only biotic data were included in the multivariate analysis, because we wanted to study ecological regime shifts (Lees *et al.*, 2006). The 0-group data and the Russian krill data were log-transformed. All data were centred to zero mean and standardized to unit variance before analysis.

Results

Temporal development in main components and drivers

Since the cold late 1970s, there has been an overall increasing trend in temperature at the FB section and in the area with SOWI (Figure 2). In the past decade, the area of Atlantic water and mixed water has increased, whereas that of Arctic water has decreased. The warming has been especially strong since the mid-1990s. There is a positive correlation between temperature and NAO from the late 1970s to the late 1990s (Figure 2, lower

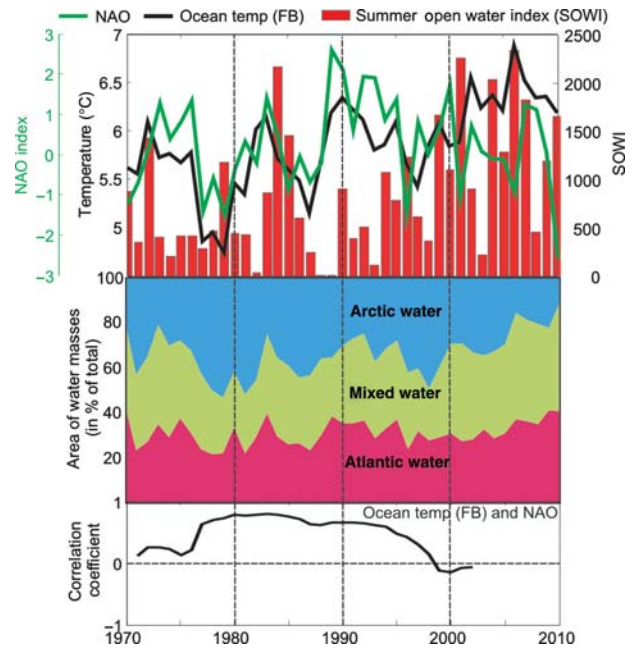


Figure 2. Temporal variation in NAO, temperature along the FB section, the area with open water (upper panel), and the relative areas of Atlantic water, mixed water, and Arctic water (centre panel). (Bottom panel) Fifteen-year sliding correlation coefficients (centred) between NAO and temperature along the FB section (the start year is 1964).

panel). Following the low NAO in 1996, the relation between NAO and temperature disappeared.

Demersal fish stock levels were high in the 1970s, but declined to historical lows in the 1980s (Figure 3). In the 1990s, the abundances fluctuated before steadily increasing in the 2000s. This development was in particular driven by the variation in cod biomass, which is currently at a level comparable with the 1950s.

In the 1970s, capelin and polar cod biomasses (no polar cod biomass data are available before 1986, but they are known from other unpublished sources) were high, and juvenile herring were absent as a consequence of the collapse in the herring stock in the late 1960s (Figure 3). The herring stock recovered in the 1980s with the appearance of the strong 1983 year class. In the mid-1980s, 1990s, and 2000s, the capelin stock collapsed, but subsequently rebuilt. The first two first capelin collapses led to an almost complete collapse of pelagic fish biomass in the BS because of the comparable low levels of the other pelagic fish stocks at the time. The early part of the 2000s was characterized by high levels of blue whiting, a typical Norwegian Sea species extending into the BS at high abundance, and high abundance of juvenile herring and polar cod. Therefore, during the capelin collapse in the 2000s, the overall biomass of pelagic fish in the BS remained high.

The biomass of krill, mesozooplankton, and shrimp has been variable (Figure 3). The shrimp stock declined abruptly in the 1980s, but both shrimp and krill have followed an increasing trend during the past two decades.

Fishing pressures on all fish stocks were high and increasing in the 1970s (Figure 4). The fishery for shrimp developed in late 1970s and peaked in the late 1980s. Following the first capelin collapse, management of the capelin fishery changed. The harvest

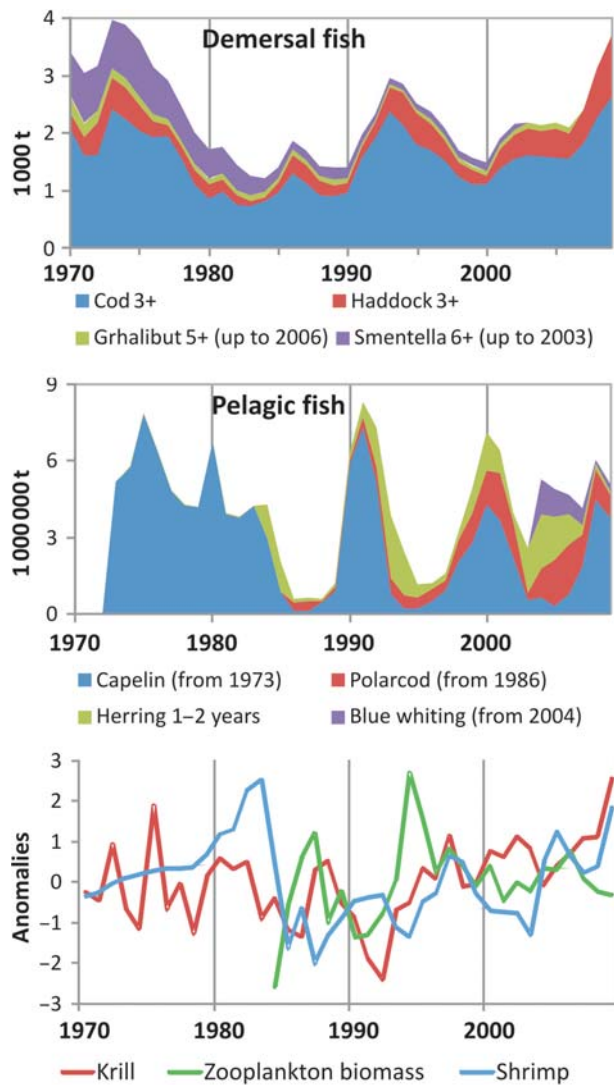


Figure 3. Temporal variation in the biomass of demersal fish (top panel), pelagic fish (middle), and mesozooplankton, krill, and shrimp (bottom). Data on polar cod were not available before 1986, but polar cod biomass is known to have been high during the 1970s. The time-series for shrimp, krill, and mesozooplankton are normalized, not added.

control rule now in force takes into account the cod stock’s need for capelin as food and allows for a smaller capelin fishery. Fishing pressure on cod and haddock was high in the 1970s and 1980s, but much lower in the late 1980s because of stock declines. The fishing pressure on cod increased to high levels by the end of the 1990s, but reduced in the past decade when a new harvest control rule was implemented (in 2004) and when illegal fishing became more strictly controlled.

Temporal development in trophic control

The correlation between total biomass of pelagic fish and krill was positive in the 1970s and 1980s, negative in the 1990s, and positive in the recent decade (Table 2, Figure 5). This suggests bottom–up control on pelagic fish by krill in the 1970s, 1980s, and the past decade, and top–down control by pelagic fish on krill in the 1990s. The correlation between pelagic fish and mesozooplankton

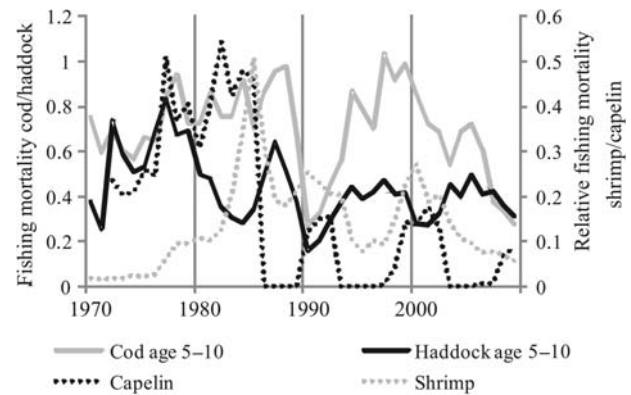


Figure 4. Temporal variation in fishing pressure represented as the fishing mortality (F_{bar} 5–10 and F_{bar} 4–7 years from assessment) for cod and haddock and the relative fishing mortality for capelin and shrimp.

was negative throughout the past three decades, suggesting persistent top–down control by pelagic fish on mesozooplankton.

The correlations between demersal fish and shrimp fluctuated over time, but overall increased from negative in the 1970s to positive in the past decade (Table 2, Figure 5). The correlation between demersal fish and pelagic fish was positive until the mid-1980s, then became increasingly negative until the later period when the correlation coefficients approached zero.

When regressing decadal mean temperatures and correlation coefficients of prey and predators by decade, the effect of temperature on trophic control was not significant ($p > 0.19$, all predator–prey correlations, $n = 4$ decades).

Temporal development in ecosystem state

The optimal number of distinct periods, based on cross-validation and chronological clustering, was 12 for the dataset from 1970 to 2009 and 4 for the dataset from 1986 to 2009 (Figure 6). The first and most important split in the 1970–2009 dataset was between the period 1970–1983 and the period 1984–2009. The split coincides with the reappearance of juvenile herring in the BS and with the first capelin/pelagic collapse (Figure 3). The clustering of the years 1986–2009 were different in the two datasets. Both analyses defined a split in 1994, coinciding with the second capelin/pelagic collapse, but the analyses differed in defining splits after 1994; the 1970–2009 dataset clustering split the period from 1994 to 2007 into four periods, whereas the 1986–2009 dataset clustering did not split the period from 1994 to 2005. Both analyses also defined a period in the past few years coinciding with maximum temperatures and minimum ice cover in the BS (Figure 2), although the split was placed differently (2006 vs. 2008).

The first principal component of the PCA (PC1) explained 26.3% and the second component (PC2) explained 24.0% of the total variation in the eight time-series starting in 1970. For the 20 time-series starting in 1986, the PC1 explained 20.4% and the PC2 17.6% of the total variation. Therefore, from our results, PC1 and PC2 seem to account for similar amounts of variability in the datasets.

The temporal trajectories of the PC1 scores were similar for the analysis run on data from 1986 and data from 1970 (Figure 7). The PC1 scores were relatively constant over time until the mid-1980s, followed by the period of ~10 years with strong variability.

Table 2. Correlations between time-series of predators and prey by decade.

Period	Demersal fish vs. pelagic fish	Demersal fish vs. shrimp	Pelagic fish vs. krill	Pelagic fish vs. mesozooplankton	Temperature (°C)
1970–1979	0.47	−0.37	0.67	–	5.47
1980–1989	−0.62	−0.62	0.29	−0.86	5.67
1990–1999	−0.39	−0.60	−0.70	−0.79	5.94
2000–2009	−0.13	0.65	0.07	−0.33	6.31

Demersal fish data are anomalies of the sum of biomass of cod and haddock (3+) and pelagic fish anomalies of the sum of biomass of juvenile herring (1–2 years) and capelin (1+). Including polar cod data (available from 1986 only) yielded similar results. Krill means the anomalies of the Russian krill series, and mesozooplankton is the anomalies in biomass data available from 1984 (Supplementary Figure S1). The decadal average temperatures at the FB section in August/September are given for comparison.

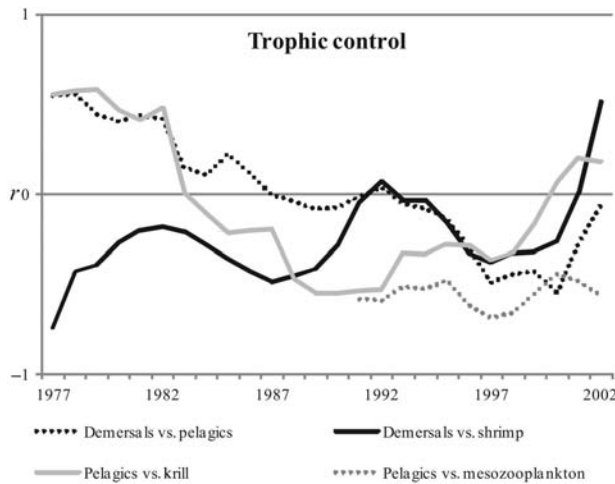


Figure 5. Correlations between predators and prey, calculated on 15-year sliding windows (centred). Pelagic fish are the sum of capelin and herring biomasses, because polar cod biomass is only available from 1986. Correlations including polar cod from 1986 on yielded similar results. Demersal fish are the sum of cod and haddock biomasses. The correlations (r) are calculated on the anomalies.

Thereafter, there has been reduced variability with a slightly increasing trend. The temporal trajectory PC2 differed among the two datasets between 1986 and the mid-1990s, but both show

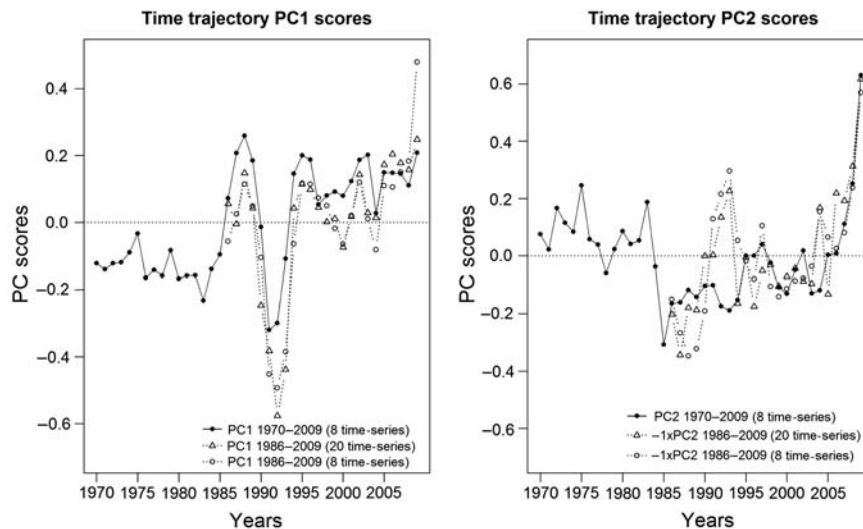


Figure 7. The results from PCA run on eight time-series from 1970 to 2009 and 20 time-series from 1986 to 2009 (Table 1), showing time-trajectories of the PC1 (left) and PC2 (right).

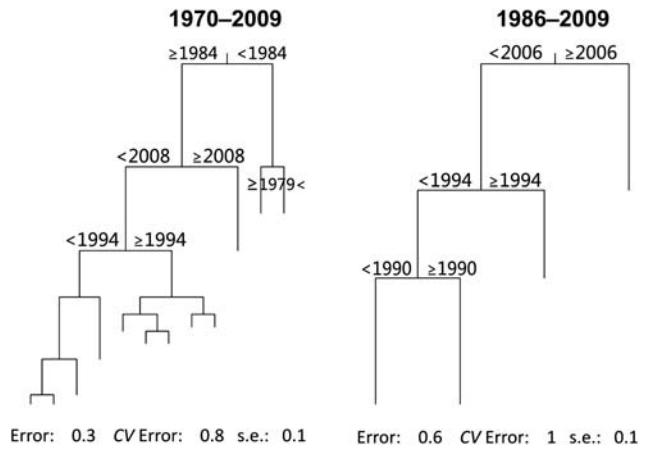


Figure 6. The optimal chronological clustering from cross-validations. The first main splits are shown for the trees based on data from 1970 to 2009 (left) and from 1985 to 2009 (right).

high variability. After the mid-1990s, the PC2 scores based on both datasets increased, especially since the mid-2000s.

Discussion

Fluctuations in trophic interactions

During the past four decades, fishing pressure in the BS has varied greatly, but overall it has been high, e.g. the average fishing

pressure on cod was higher in the BS than in the ESS (1950–1990; Sinclair, 1996), where the cod stock collapsed. The climate has varied substantially and so have stock levels. Trophic regulation also varied. Ciannelli *et al.* (2006) and Yaragina and Dolgov (2009) concluded that the BS was generally controlled by pelagic fish, with a top–down effect on zooplankton and a bottom–up effect on demersal fish. However, their conclusions were based on a period (1980–1990) with strong fluctuations in the capelin stock and comparable low biomasses of the other pelagic fish in the BS. Here, we investigated trophic interactions for an extended period including the recent warming, when interactions seem to be changing.

A complicating factor in interpreting changes in correlations between biomasses of predators and prey is the biomass removals by fishing, and in the BS, both demersal and pelagic fish have been heavily exploited. Fluctuations in the capelin stock are influenced by both fishing and top–down predation, although a recent study by Hjermann *et al.* (2010) indicates that the top–down effects attributable to predation from both juvenile herring and cod are much more important in determining the dynamic of the BS capelin than fishing. This implies that the changing predator–prey correlations may mostly be attributed to ecological processes. However, the study cited above did not include the period before the first capelin collapse (the 1970s). The high fishing pressure on both demersal fish and capelin in the 1970s could have contributed to the overall positive correlations between pelagic fish and demersal fish in that period.

The overall change towards more bottom–up control in the warm decade from the 1980s and 1990s is consistent with the findings by Frank *et al.* (2007) and Petrie *et al.* (2009) that warmer systems have more bottom–up control. The mechanisms involved are increased metabolic rates and response times at all trophic levels, and increased diversity reducing the interaction strength and the impact of reductions of single stocks attributable to, e.g. fishing (Frank *et al.*, 2007). The high abundance at the trophic level of pelagic fish found in the BS the past decade, despite a capelin collapse, illustrates the latter mechanism and was observed as a lack of negative effect on predators by the most recent capelin stock collapse (Gjøsæter *et al.*, 2009).

Our results therefore demonstrate that trophic relationships in the BS are more complex than previously inferred and that they are dynamic over time.

Regime shifts in the BS?

Our chronological cluster analyses defined many periods, although many were not consistent between the two datasets. However, three splits (1984, 1994, and 2006/2008) define important periods in the BS ecosystem that differ in relative abundance of main stocks and interactions. These periods are also apparent from the temporal development in PC scores. In the period 1970–1983, there was no herring in the BS (the herring stock collapsed in the late 1960s), but there was a high level of capelin. The period ended with the appearance of the strong 1983 herring year class, and a subsequent capelin/pelagic collapse, and it can be defined as a separate ecological regime as in Lees *et al.* (2006). The next split (1994) defines the period including the two first capelin collapses. In that period, the recruitment of cod and herring were both positively correlated with temperature and fluctuated greatly. Predation by strong year classes of cod and herring created lagged negative effects on the capelin stock, which consequently also showed large variations (Hjermann *et al.*, 2010).

Capelin are short-lived with high fecundity, and the stock rebuilt quickly after the stock collapses. The dominance of capelin at the trophic level of pelagic fish contributed to the strong, high-frequency variability that defines that period. The period thereafter, from 1994 and until the last years, coincides with rebuilding of pelagic stocks and increasing temperatures. The last split (2006–2008) defines the years of the study period co-occurring with enhanced warming in the BS.

We tested for regime shifts using chronological clustering on two datasets and because the results differed between them, no firm conclusion can be drawn. Moreover, all periods defined by the cluster analysis applied on the longest time-series were too short (<10 years) to constitute alternative ecological regimes as defined by Lees *et al.* (2006). Rather, our analysis indicates several high-frequency abrupt shifts. We found no indication of ecosystem hysteresis and we are not aware of any feedback mechanisms that could be involved. On the contrary, the BS cod stock has responded positively and fast to reductions in fishing pressure. Owing to a lack of overlap (dietary and spatial) between cod eggs and larvae and the main prey, capelin, the potential for prey–predator role reversal, a mechanism proposed to be important in hysteresis (Fauchald, 2010) seem limited in the BS.

Warming effects on BS ecosystem

The past decade has been the warmest on record (Levitus *et al.*, 2009). In the southern BS, oceanic heat transport into the area has increased (Smedsrud *et al.*, 2010), so expanding the Atlantic region and contracting the Arctic region, as observed here. After the drop in 1996, the well-documented correlation between NAO and temperature breaks in the BS, and the warming trend increased despite a weaker NAO index. Hence, the decade of the 2000s is distinguished from earlier decades in the oceanographic processes. The mechanism driving the recent warming in the BS is not yet fully understood.

In the same period, we found evidence for increased bottom–up regulation and an ecosystem that sustained large stocks of demersal and pelagic fish and increasing biomasses of shrimp and zooplankton, indicating increased productivity that can be related to the warming. Other studies also show evidence of the effect of warming on the BS ecosystem, e.g. the onset of the primary production (the spring bloom) may start 50 days earlier in the northeastern BS compared with 10 years ago (Kahru *et al.*, 2011).

Although good time-series data on many species are lacking, there are indications that warming increases the distribution range within the BS of southerly warm-water species and decreases the area or habitat for the Arctic species. The krill *M. norvegica* has extended its distribution northwards and is now commonly found also in the BS (Zhukova *et al.*, 2009). There are also indications that the abundance of the Arctic species *T. libellula* has decreased during the past decade, in turn affecting higher trophic levels that depend on this species as prey (Dalpadado and Mowbray, *in press*). Cod have extended their distribution north in the BS during the past decade, possibly as a response to the warming (G. O. Johansen, pers. comm.). Further, blue whiting, which are associated with warmer water, were present in large numbers in the past decade, although their abundance has declined in recent years (Heino *et al.*, 2008; Dolgov *et al.*, 2010). Also, warm-water fish such as snake pipefish (*Entelurus aequoreus*) have appeared in the BS for the first time during the past decade (Dolgov *et al.*, *in press*).

Under warming conditions, trophic interactions in the ecosystem could weaken as a result of increased diversity at each trophic level caused by range expansion of species found in warmer areas. The lack of effect of the last capelin collapse on its predators indicates weakened interactions. In addition, the herring–capelin interaction seems to have weakened, because capelin recovered after the collapse in the 2000s despite the presence of large numbers of juvenile herring. The weakening of the herring–capelin interaction is possibly caused by reduced spatial overlap, which at least partly could be related to recent changes in preferred spawning grounds for capelin. Although in earlier decades, cold years were associated with westerly spawning of capelin, the recent warm decade was associated with extreme westerly distribution of spawning capelin (Carscadden *et al.*, in press). Other temperature relations have also changed in the past decade. Previously, warmer-than-average years were associated with strong year classes of cod (Stiansen *et al.*, 2005), but during the past decade, cod recruitment has been below average (ICES, 2010a). Our examples of recent changes in well-known relationships between species, as well as between temperature and various biological parameters, demonstrate the challenge in predicting effects of future climate change from former relationships in a highly dynamic system.

Supplementary material

Supplementary material is available at the ICES/JMS online version of this manuscript in the form of time-series data lists, units, and references (Supplementary Tables S1–S3), and presented as colour anomalies (Supplementary Figure S1).

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