

# Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s

J. Alheit, C. Möllmann, J. Dutz, G. Kornilovs, P. Loewe, V. Mohrholz, and N. Wasmund

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The index of the North Atlantic Oscillation, the dominant mode of climatic variability in the North Atlantic region, changed in the late 1980s (1987–1989) from a negative to a positive phase. This led to regime shifts in the ecology of the North Sea (NS) and the central Baltic Sea (CBS), which involved all trophic levels in the pelagial of these two neighbouring continental shelf seas. Increasing air and sea surface temperatures, which affected critical physical and biological processes, were the main direct and indirect driving forces. After 1987, phytoplankton biomass in both systems increased and the growing season was extended. The composition of phyto- and zooplankton communities in both seas changed conspicuously, e.g. dinoflagellate abundance increased and diatom abundance decreased in the CBS. Key copepod species that are essential in fish diets experienced pronounced changes in biomass. Abundance of *Calanus finmarchicus* (NS) and *Pseudocalanus* sp. (CBS) fell to low levels, whereas *C. helgolandicus* (NS) and *Temora longicornis* and *Acartia* spp. (CBS) were persistently abundant. These changes in biomass of different copepod species had dramatic consequences on biomass, fisheries, and landings of key fish species: North Sea cod declined, cod in the CBS remained at low levels, and CBS sprat reached unprecedented high biomass levels resulting in high yields. The synchronous regime shifts in NS and CBS resulted in profound changes in both marine ecosystems. However, the reaction of fish populations to the bottom-up mechanisms caused by the same climatic shift was very different for the three fish stocks.

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J. Alheit, J. Dutz, V. Mohrholz, and N. Wasmund: Baltic Sea Research Institute, Seestrasse 15, D-18119 Warnemünde, Germany. C. Möllmann: Danish Institute for Fisheries Research, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark. G. Kornilovs: Latvian Fisheries Research Agency, Daugavgrivas Street 8, LV-1007 Riga, Latvia. P. Loewe: Bundesamt für Seeschifffahrt und Hydrographie, Bernhard-Nocht-Strasse 78, D-20359 Hamburg, Germany. Correspondence to J. Alheit: tel: +49 381 5197 208; fax: +49 381 5197 440; e-mail: [juergen.alheit@io-warnemuende.de](mailto:juergen.alheit@io-warnemuende.de).

## Introduction

Evidence is accumulating that marine ecosystems undergo large-scale, decadal fluctuations which seem to be driven by climate forcing (Stenseth *et al.*, 2002), as clearly demonstrated for the North Pacific (e.g. Hare and Mantua, 2000) and eastern boundary current systems (e.g. Chavez *et al.*, 2003; Alheit and Niquen, 2004). Shifts in climate regimes can reorganize marine communities and trophodynamic relationships, and induce changes in the mix of dominating species over decadal time scales. During a Workshop on Regime Shifts in Villefranche-sur-Mer in April 2003, regime shifts in the marine realm were defined in a pragmatic

way as “changes in marine system functioning that are relatively abrupt, persistent, occurring at a large spatial scale, observed at different trophic levels, and related to climate forcing” (deYoung *et al.*, 2004). In contrast to a purely climatic regime shift, which might happen within a very short period, an ecological regime shift cannot necessarily be pinpointed to one or two single years. The reason behind this is that the response of marine populations to physical forcing is often delayed owing to complex recruitment processes. A difference in the timing of the shift of different populations can also be expected as different species react differently to climatic forcing, depending on their particular physiological threshold values and their life history traits

(Beaugrand and Reid, 2003; Beaugrand, 2004). An ecological regime shift in the North Sea in the late 1980s has been extensively described in a large number of publications and has been related to changes in the index of the North Atlantic Oscillation (NAO) (Reid *et al.*, 1998b, 2001a, b, 2003; Kröncke *et al.*, 2001; Reid and Edwards, 2001; Beaugrand and Ibanez, 2002; Beaugrand *et al.*, 2002, 2003; Reid and Beaugrand, 2002; Beaugrand, 2003, 2004; Beaugrand and Reid, 2003).

The NAO influences the entire northern European region, and changes in the dynamics of physical and biological variables have been observed in the central Baltic Sea around 1987–1989. This study investigates whether a similar ecological regime shift occurred in the Baltic Sea, and how it compares with observations reported from the North Sea.

## Material and methods

The North Sea and the Baltic Sea are two neighbouring continental shelf seas that exhibit very different hydrographic structures (Figure 1). Long-term data series of biological and physical variables from both ecosystems were extracted from a number of publications and databases (Table 1), analysed, and compared with each other. The long-term North Sea temperature time-series from Helgoland Roads was obtained from the German Federal Maritime and the Hydrographic Agency in Hamburg (Bundesamt für

Seeschifffahrt und Hydrographie). The Baltic Sea (Bornholm Sea, Station K2) temperature data series was constructed from ICES databases, the Baltic Sea Research Institute at Warnemünde, and the German GLOBEC project ([www.globec-germany.de](http://www.globec-germany.de)). Long-term zooplankton data were compiled by the Latvian Fisheries Research Agency (LATFRA) in Riga.

## Results

### North Atlantic Oscillation

The North Atlantic Oscillation (NAO) is the dominant mode of climatic variability in the North Atlantic region. Decadal NAO variability influences regional temperatures, precipitation, windspeed, and wind direction over northern Europe (Hurrell, 1995). A high (low) NAO index is associated with increased (decreased) westerly winds and milder (cooler) temperatures over northern Europe. Besides the associated windforcing, the impact of the NAO on the marine ecosystems is mainly through the heat flux exchange between the atmosphere and the ocean, which controls the temperature of the upper mixed layer. Variability in the winter NAO (January/February) index is clearly mirrored by surface temperatures of the North Sea (Helgoland Roads series) and the Intermediate Winter Water (IWW) of the central Baltic Sea (Figure 2). There is a strikingly coherent

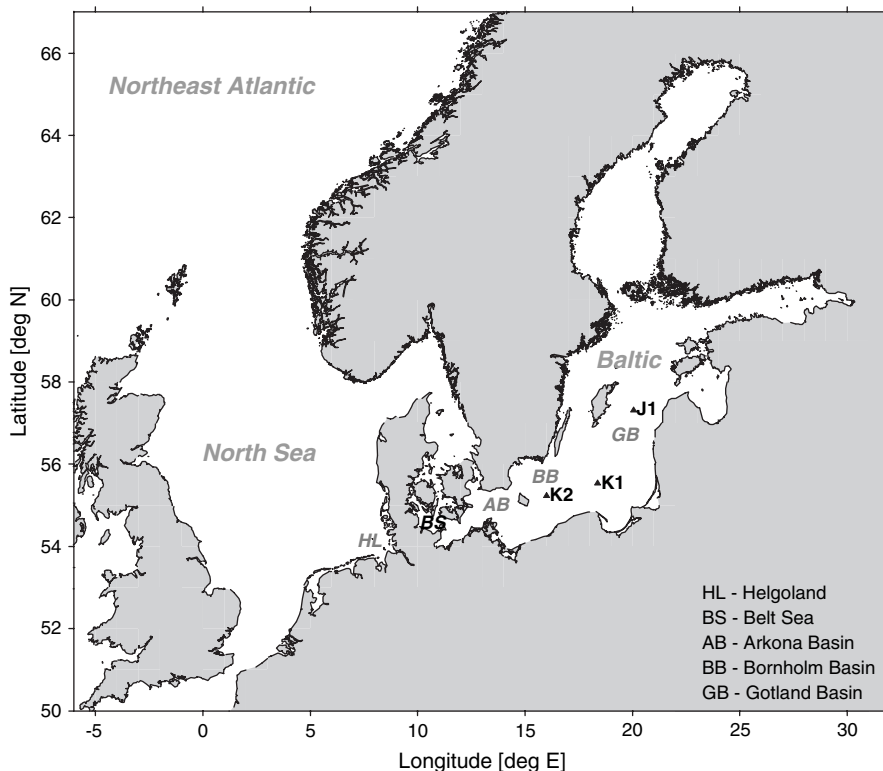


Figure 1. Map of the investigation area. K1, K2, and J1: stations of the HELCOM long-term plankton monitoring.

Table 1. Sources of long-term data series.

Time-series	Source
SST Helgoland Roads	Loewe <i>et al.</i> (2003)
NAO winter index	Modified from <a href="http://www.cru.uea.ac.uk">http://www.cru.uea.ac.uk</a>
Annual temperature minimum in the IWW of the Bornholm Basin (Station K2)	Baltic Sea Research Institute, <a href="http://www.ices.dk">http://www.ices.dk</a>
Monthly mean temperature difference [ $^{\circ}\text{C}$ ] in the central Bornholm Basin (Station K2)	Baltic Sea Research Institute, <a href="http://www.ices.dk">http://www.ices.dk</a>
Annual temperature maximum in the halocline (55–70 m of the Bornholm Basin, Station K2)	Baltic Sea Research Institute, <a href="http://www.ices.dk">http://www.ices.dk</a>
Phytoplankton spring biomass in the Bornholm Basin (Station K2) and the Gotland Basin (Station K1)	Wasmund <i>et al.</i> (1998)
Diatom and dinoflagellate biomass in the Gotland Basin (Station J1)	Wasmund and Uhlig (2003)
Silicate concentration in the Bornholm Basin (Station K2) and Gotland Basin (Station K1)	Wasmund <i>et al.</i> (1998)
Biomass anomalies of <i>Acartia</i> spp., <i>Temora longicornis</i> , and <i>Pseudocalanus</i> sp. in the Gotland Sea and the Gdansk Deep	Möllmann <i>et al.</i> (2003b)
Biomass and recruitment of sprat	ICES (2002)

increase in the values of all three time-series from 1987 to 1989. Since 1989, with the exception of the cold year of 1996, the values of all three time-series have been comparatively high. However, it should be noted that the variability of the summer and autumn NAO might differ considerably from the winter NAO. Indeed, in the 1990s, the NAO in summer and autumn did not exhibit the same positive increase as in winter (<http://www.cru.uea.ac.uk>).

### North Sea

An ecological regime shift occurred in the North Sea ecosystem in the late 1980s that affected all trophic levels

including phytoplankton, zooplankton, and benthos to fish (Reid and Edwards, 2001). It has been linked to a shift to a positive NAO index that coincided with an increased incursion of warm oceanic water from the Atlantic into the northern North Sea (Edwards *et al.*, 2001; Reid *et al.*, 2001a; Beaugrand, 2003). Modelling has shown increased winter inflow in the upper layer (0–150 m) into the North Sea since 1988 (Reid *et al.*, 2003). Enhanced inflows are generated by increased westerly winds that reflect regional changes in the climate of northwest Europe, and are highly correlated with the NAO (Reid *et al.*, 2003).

The ecological regime shift in the late 1980s led to an exceptional period in a 52-year time-series, as demonstrated

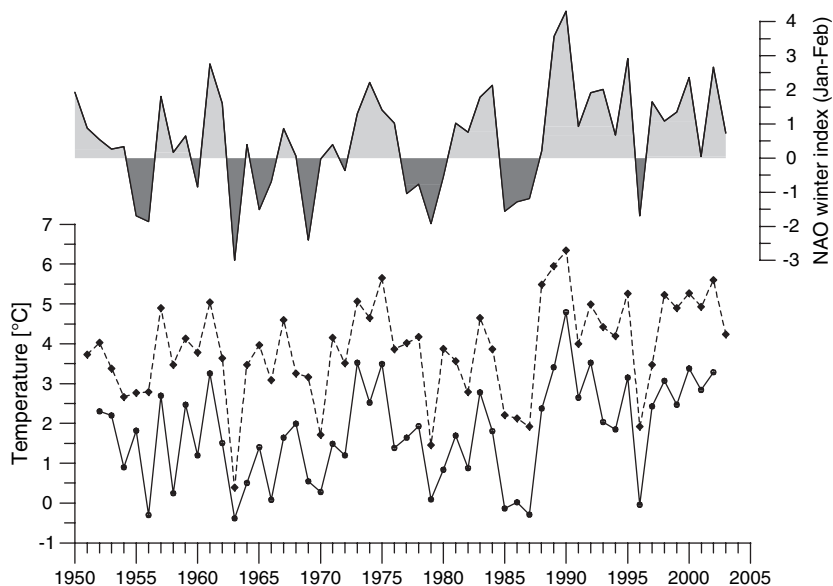


Figure 2. NAO winter index (modified from <http://www.cru.uea.ac.uk>), annual temperature minimum in the Intermediate Winter Water (IWW) of the Bornholm Basin, Station K2, (solid line), and mean winter SST (January to March) at Helgoland Roads (dashed line) (Loewe *et al.*, 2003).

by a cluster analysis performed on physical and biological variables (Beaugrand and Reid, 2003).

#### *Phytoplankton*

Long-term changes in phytoplankton colour, a visual index of chlorophyll from the Continuous Plankton Recorder (CPR) (Reid *et al.*, 1998a), are considered to be indicators of changes in primary production (Beaugrand and Reid, 2003). After 1987, phytoplankton colour, averaged for three areas in the North Sea, increased substantially, both in level and seasonal extent (Edwards *et al.*, 2001; Reid *et al.*, 2001a; Beaugrand and Reid, 2003). Many phytoplankton species showed marked changes in abundance at about the same time (Reid *et al.*, 2001a). Dinoflagellates became more abundant in the late 1980s, and the long-term trend of dinoflagellate abundance was positively correlated with the NAO index (Edwards *et al.*, 2002; Drinkwater *et al.*, 2003).

#### *Zooplankton*

After 1987, many species of zooplankton also exhibited pronounced changes in abundance (Reid *et al.*, 2001a). High positive anomalies in the abundance of *C. helgolandicus* were recorded, whereas negative anomalies were observed for *C. finmarchicus* (Beaugrand, 2003). In general, copepod species composition and diversity changed (Beaugrand and Ibanez, 2002; Beaugrand, 2003), whereby warm-water species increased and cold-water species decreased (Beaugrand, 2004). In a principal component analysis of 30 taxonomic entities, the first component showed a marked stepwise increase around 1988 (Reid *et al.*, 2001a).

#### *Benthos*

Since 1988, an increase in abundance, species number, and biomass of macrofauna was recorded off the island of Norderney in the second quarter of the year (Kröncke *et al.*, 2001). Also around 1989, pronounced changes in the benthic community composition occurred off the northeast coast of England (Reid and Edwards, 2001).

#### *Fish*

After 1987, catches of the western stock of horse mackerel (*Trachurus trachurus*) showed a large increase in the northern North Sea owing to a northerly expansion of the stock along the shelf edge from the Bay of Biscay to the North Sea (Reid *et al.*, 2001a). Since about 1987, cod recruitment has been affected negatively in the North Sea by a severe reduction of both quantity and quality of their larval food (Beaugrand *et al.*, 2003).

### Baltic Sea

#### *Temperature regime*

In the central Baltic Sea, the intensity of winter cooling controls the onset of thermal stratification in spring. Salinity has only a minor effect on density stratification above the halocline, since its variations are small in the well-

mixed surface layer. When the minimum SST in winter is well below the density maximum of seawater, the first heating of the surface layer causes a vertical convection until the SST exceeds the temperature of the density maximum. After mild winters, when the SST is not below the temperature of the density maximum, the first heating in spring leads directly to thermal stratification of the surface layer. Before 1988, the minimum wintertime SST in the Baltic was usually below the temperature of the density maximum (Figure 2). As a consequence of the increase of the NAO index since 1989, the minimum SST in winter stayed above the temperature of the density maximum, with the exception of 1996. This shift in winter SST appears to have induced pronounced changes in the ecosystem.

To demonstrate the hydrographic change in the central Baltic Sea, we compared the climatological temperature time-series for the periods 1970–1987 and 1988–2003 using data from the Bornholm Basin (Figure 3). The temperature differences are based on monthly means. The most prominent pattern is the increase in the spring and autumn surface mixed layer temperatures by about 1.5 °C. The summer maxima also increased by ~1 °C. Moreover, in the halocline (50–60 m), an increase in temperature (~1 °C) was observed throughout almost the entire year. In contrast, the temperature in the deep layers of the Bornholm Basin (below 70 m) remained the same during both periods.

Whereas the increase in the Baltic SST can be linked directly to heat fluxes associated with the positive phase of the NAO, the higher temperatures in the halocline appear to be associated with changes of the summer inflow conditions in the transition area between the Baltic and the North Sea (Feistel *et al.*, 2003). In summer, a mean estuarine flow regime is established in the Baltic Sea with an outflow of brackish Baltic surface water and an inflow of saline North Sea water at the bottom, with salinities of 6 to 10 psu and 15 to 25 psu, respectively. Frequently occurring wind events can force mixing between these water masses, which lowers the salinity of inflowing water. However, in some years with weak windforcing in summer, the salinity of the inflowing water remains high owing to the lack of mixing. In this situation, the inflowing denser water can reach the halocline layers in the central Baltic Sea, resulting in anomalously high temperatures. The annual maximum temperatures in the halocline layer of the Bornholm Basin increased after 1987, suggesting a corresponding increase in the frequency of years with warm-water inflows into the halocline of the central Baltic Sea (Figure 4). The exceptional warm summer inflow in 2002 has been described in detail by Feistel *et al.* (2003). To understand why there are years with weak windforcing in summer in spite of the high winter NAO index since the late 1980s, one has to bear in mind that (i) the strong influence of the NAO, particularly in the Baltic area, is exerted mainly in winter and (ii) since the 1980s, the NAO index was mainly negative in summer and autumn.

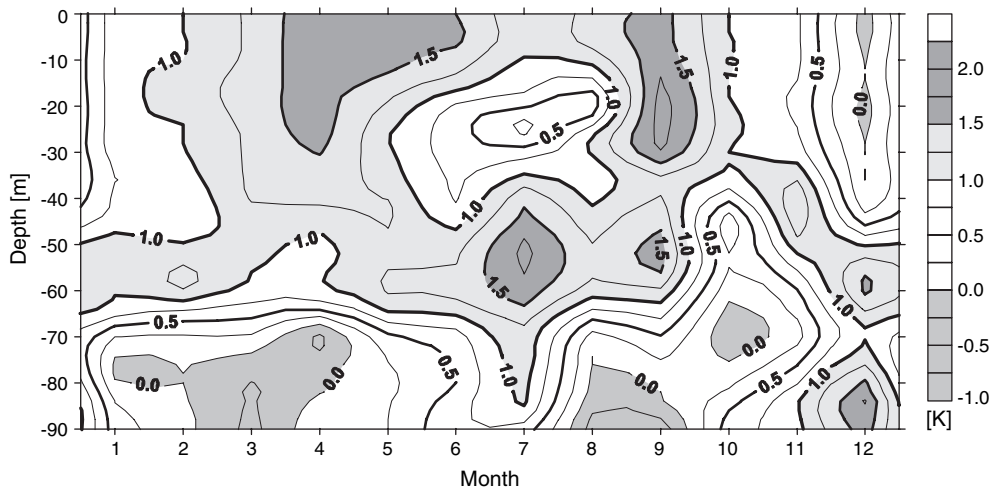


Figure 3. Monthly mean temperature difference (K) in the central Bornholm Basin (Station K2) between the periods 1970–1987 and 1988–2003.

#### Phytoplankton

Long-term variation in spring phytoplankton biomass from 1979 to 1996 in the Bornholm Basin and in the southern Gotland Basin shows a drastic increase since 1987/1988 (Figure 5) (Wasmund *et al.*, 1998). However, the interannual differences should be considered with a certain reservation as the data sets are not homogeneous, and the number of samples is rather low. In the Bornholm and southern Gotland Seas, the spring diatom biomass dropped dramatically from 1988 to 1989 and stayed at this low level, whereas dinoflagellate biomass showed a steady increase from 1989 onward (Figure 6) (Wasmund and Uhlig, 2003). As all the biomass data rely on a rather small number of field samples, which are more or less snapshots, it is necessary to confirm this decrease of diatoms using indirect methods. Consumption of silicate has been shown to be an excellent proxy for diatom growth. As diatoms are the only organisms that incorporate silicate in significant quantities in the central Baltic Sea, their increase in biomass should result in a decrease of silicate in the water. Long-term time-series of (i) silicate concentration in surface waters in late winter and (ii) the difference in pre-bloom and post-bloom silicate concentrations

have been constructed by Wasmund *et al.* (1998) for the period 1980–1999 for the Bornholm Basin (Station K2) and the southern Gotland Basin (Station K1) (Figure 7). Whereas the curve of the late winter silicate concentrations exhibited only slight variations over this time span, silicate consumption (difference between pre- and post-bloom concentrations) started to decrease considerably in 1988 (southern Gotland Basin) and particularly in 1989 (Bornholm Basin), and remained at very low levels until 1999. The long-term decrease of diatom biomass and the increase of dinoflagellate biomass (Figure 6), together with the reduction of phytoplankton biomass (Figure 5), coincide with the increase of surface temperature in the central Baltic Sea since the late 1980s (Figures 2 and 3). As in the North Sea, the phytoplankton spring bloom also seems to have shifted to an earlier start in the Baltic Sea, as demonstrated for the Kattegat (HELCOM, 1996, 2002).

#### Copepods

The copepod community of the central Baltic Sea is dominated by *Pseudocalanus* sp., *Temora longicornis*, and

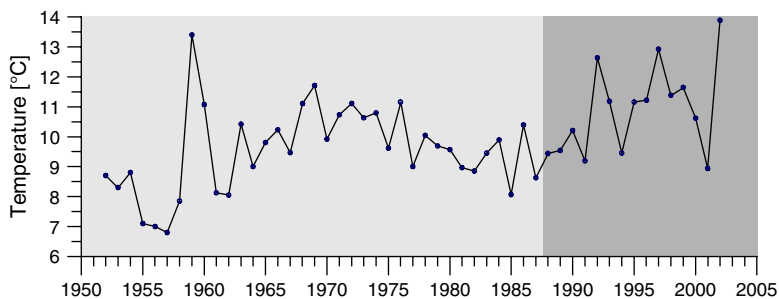


Figure 4. Annual temperature maximum in the halocline (55–70 m) of the Bornholm Basin (Station K2).

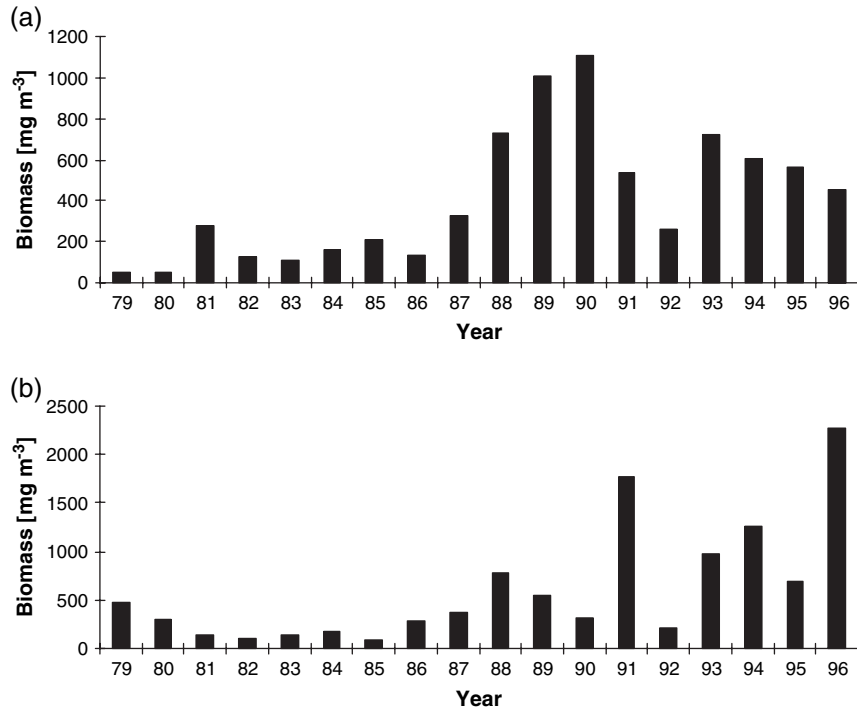


Figure 5. Mean biomass (wet weight) of spring phytoplankton (March–May) in surface waters (mean of 0–10 m depth) from 1979 to 1999 in the (a) Bornholm Basin (Station K2) and (b) Gotland Basin (Station K1). Modified after *Wasmund et al. (1998)*.

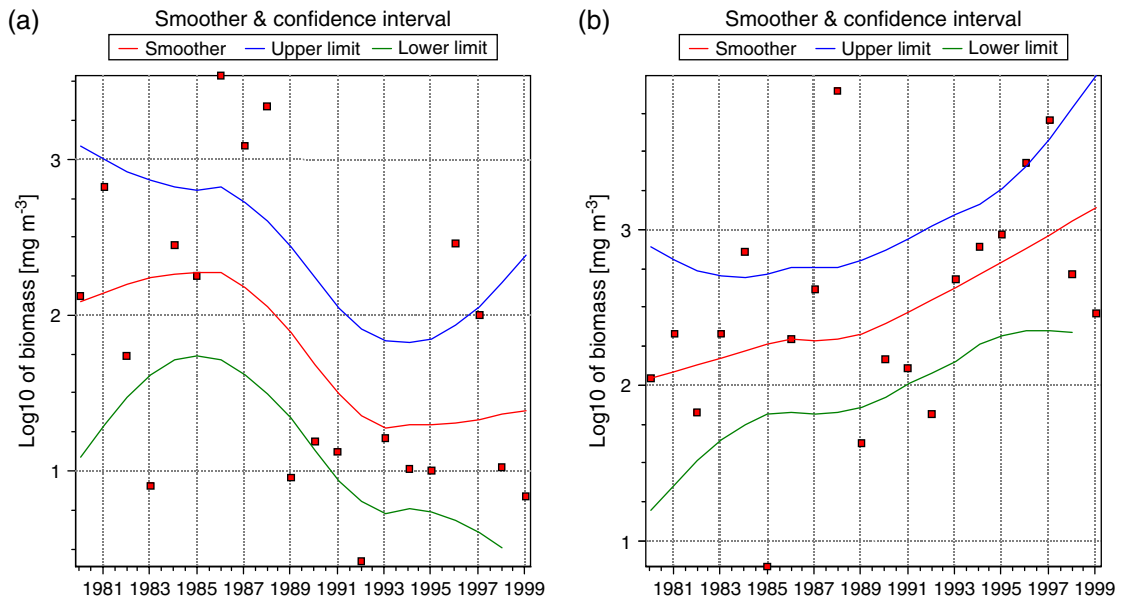


Figure 6. Trend in (a) diatom (in  $\text{mg m}^{-3}$ , given as  $\log_{10}$  data, means March–May) and (b) in dinoflagellate biomass in Gotland Sea (Station J1). Upper and lower lines represent the limits of the approximate pointwise 95% confidence limits for the trend line. Modified after *Wasmund and Uhlig (2003)*.

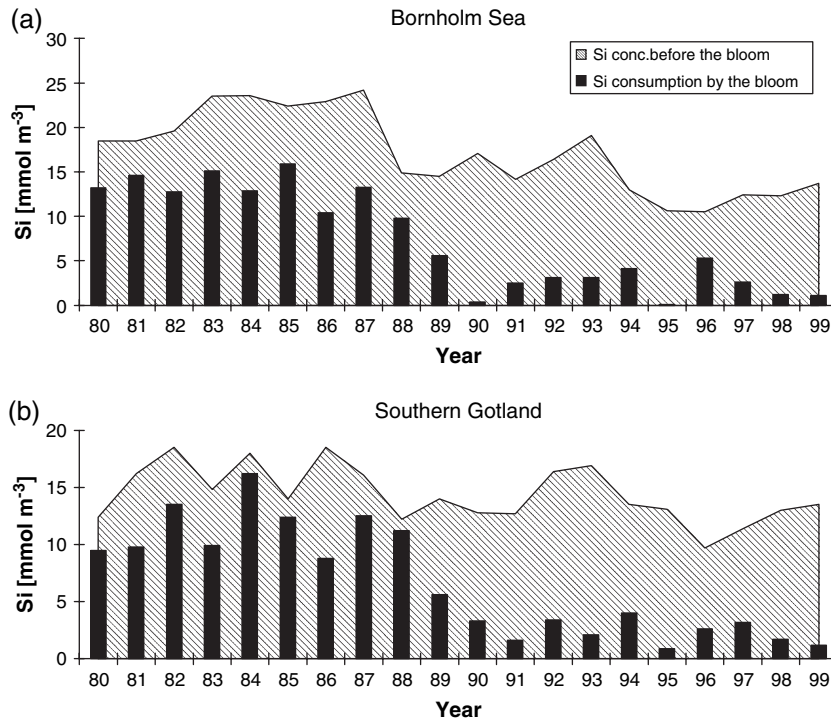


Figure 7. Surface water silicate concentration in late winter (curve) and difference in pre- and post-bloom silicate concentrations (bars) from 1979 to 1996 in (a) Bornholm Basin (Station K2) and (b) Gotland Basin (Station K1). Modified after Wasmund *et al.* (1998).

*Acartia* spp., the different stages of which constitute the main food items for larvae of the three dominant fish species, cod, herring, and sprat (Hinrichsen *et al.*, 2002; Voss *et al.*, 2003), and also for juvenile and adult sprat and herring (Möllmann *et al.*, 2004). Atmospheric forcing has a pronounced influence on the spring population of mesozooplankton species in the central Baltic (Möllmann *et al.*, 2000). Spring biomass anomalies of *T. longicornis* and *Acartia* spp. from 1960 to 2000 exhibited very similar variability, with negative anomalies from 1960 to the late 1980s and positive anomalies in the 1990s (Figure 8), with a dramatic increase in the late 1980s. In contrast, *Pseudocalanus* sp. showed a very different pattern (Figure 8), with relatively low biomass values in the 1960s, followed by a biomass increase in the early 1970s that culminated in the first half of the 1980s. Thereafter, biomass decreased almost continuously.

#### Fish

Cod, herring, and sprat (ages 1+) in the central Baltic Sea showed pronounced long-term variability (Figure 9) (Köster *et al.*, 2003b). Whereas herring abundance was relatively stable on a low level from 1970 to 2000, cod and sprat abundances changed drastically, but in an inverse manner. Cod abundance peaked in the late 1970s and early 1980s and reached historic low values in the 1990s. Sprat, however, after very low abundance in the 1980s, began to

rise in 1988/1989, just when cod reached its lowest stock sizes (Köster *et al.*, 2001). Anomalies of biomass and recruitment of sprat (ICES, 2002) began to increase in the late 1980s (Figure 10).

## Discussion

Ecological regime shifts occurred in the North Sea and the central Baltic Sea synchronously in the late 1980s. These shifts seem to have been a response to the NAO, the winter index of which entered a positive phase characterized by elevated temperatures and stronger westerly winds. In spite of very different hydrographic characteristics between the two ecosystems and different responses of populations to changes in the NAO, response to the regime shifts in both systems is strikingly similar, affecting all trophic levels in the pelagial. Phytoplankton biomass increased and the growing season was extended. Abundance of key copepod species that are essential food for key fish populations exhibited conspicuous coherent increases or decreases with the NAO. This contributed to a reduction in recruitment of North Sea cod, whereas Baltic sprat started to thrive, with resulting strong impacts on fisheries and landings of both species.

Temperature, which is highly correlated with NAO variability, seems to be the key physical variable impacting

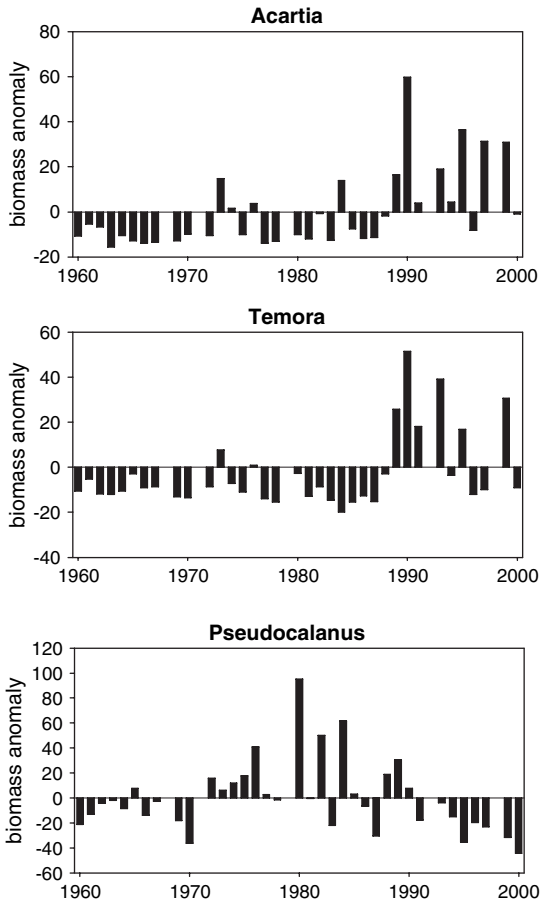


Figure 8. Biomass anomalies of the copepods *Acartia* spp. (upper panel), *Temora longicornis* (central panel), and *Pseudocalanus* sp. (lower panel) from the Gotland Sea and the Gdansk Deep.

phytoplankton, zooplankton, and fish species in both systems. However, besides direct impacts on marine organisms (e.g. by enhancing growth, reproduction, and related physiological rates) indirect effects through a chain of interwoven physical and biological processes also appear to be triggered by increasing air and sea temperatures. Significant correlations between climate indices and biological processes are consistent with climate variability forcing changes in biological variables and processes. We note that these observations do not prove causal relationships.

Since the North Sea regime shift has been adequately described (see previous list of references), the focus of this discussion is on processes in the Baltic Sea.

#### Diatoms/dinoflagellates

Causes of the diatom decline in the central Baltic Sea may be caused by the relatively high winter water temperatures recorded since the late 1980s (Figures 2 and 3). However, its influence is not the direct impact of temperature on algae, which seems to be decisive, but its influence on water stratification (Wasmund *et al.*, 1998). In cold winters, the water typically cools to the temperature of maximum density, e.g. 2.5°C at a salinity of 7 psu, and the surface mixed layer extends down to the permanent pycnocline. A further decrease in temperature leads to a new stabilization of the water column. As the surface water warms in spring, convective mixing down to the permanent pycnocline occurs initially, followed later by a stabilization and stratification of the water column. Diatoms need mixed waters, whereas flagellates take advantage of a stable water column (Harrison *et al.*, 1986). Therefore, the phytoplankton growing season starts with a short diatom bloom during spring overturn, followed by dinoflagellate growth in the stabilization phase

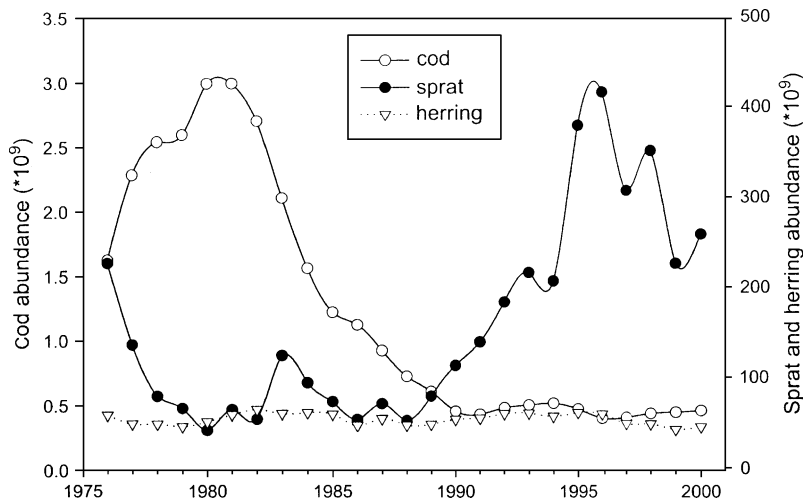


Figure 9. Abundance of cod, sprat, and herring (age group 1+, beginning of the year) in the central Baltic Sea. Modified after Köster *et al.* (2003b).



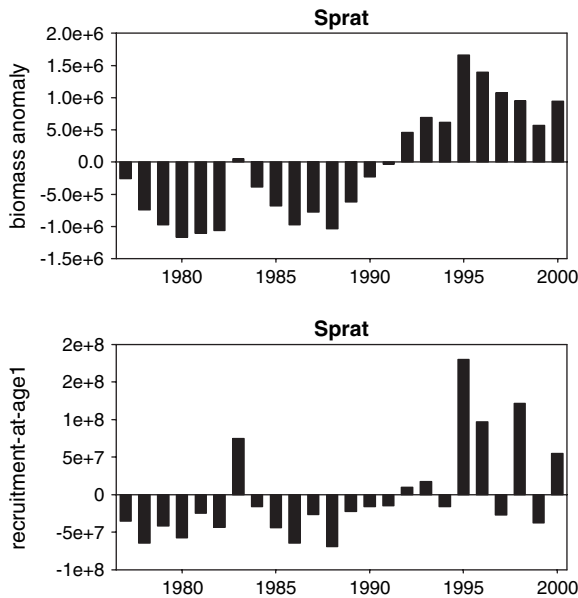


Figure 10. Biomass anomalies and recruitment of sprat (at age 1) in the central Baltic Sea. After ICES (2002).

in the central Baltic (Wasmund *et al.*, 1998). In mild winters, water temperature does not decrease to the temperature of maximum density. No deep convective mixing occurs, and stabilization of the water column begins with the first signs of heating. The lack of spring overturn inhibits diatoms, but promotes the growth of dinoflagellates. When the diatom bloom fails, the dinoflagellates not only fill this gap, but their biomass tends to more than compensate for the loss in diatom biomass. Overall, spring values of chlorophyll *a* showed an increasing trend at Stations K1 and K2 (Wasmund *et al.*, 1998). Interestingly, increased abundance of dinoflagellates recorded in the North Sea since the late 1980s was also related to changes in stratification (Edwards *et al.*, 2002; Drinkwater *et al.*, 2003).

### Copepods

Shifts in long-term copepod abundances in both the North Sea and the central Baltic ecosystems partly reflect temperature changes, and thus climate forcing (Möllmann *et al.*, 2000; Beaugrand and Reid, 2003). In the Baltic, this is particularly true for species that dwell in the uppermost layers, i.e. *Acartia* spp. and *T. longicornis*. In contrast, other species, such as *Pseudocalanus* sp. and *Oithona similis*, which live in the permanent halocline, depend strongly on the salinity level (Möllmann *et al.*, 2003b; Hansen *et al.*, 2004).

Experimental work demonstrates that hatching of nauplii from the resting eggs hibernating in the sediment is the most important source of *Acartia* spp. nauplii in spring. Laboratory experiments further show that the hatching of nauplii from resting eggs hibernating in the sediment is

strongly controlled by temperature (Dutz *et al.*, 2004). Over a temperature range of 4–10°C, which resembles the natural variation in the Intermediate Winter Water (IWW; Figure 2) above the sediments where resting eggs are deposited in the Bornholm Sea (compare Figure 3), increasing temperatures resulted in a two- to fivefold increase in the number of nauplii hatching from the sediment (Figure 11). Another potential reason for the increase of *Acartia* spp. and *T. longicornis* populations might be changes in foodweb processes as indicated by a switch from diatom to dinoflagellate dominance in the late 1980s. Although the food spectra of Baltic copepods remain unclear, there is increasing evidence that prevailing food can strongly influence the population dynamics of copepods. Recent findings suggest that diatoms exert a strong negative effect on hatching success of copepod eggs, and thus might impair recruitment of the first generation of copepods in the sea (Ianora *et al.*, 2004). Unlike diatoms, dinoflagellates and heterotrophic protists seem to favour copepod production (Kleppel, 1993; Broglio *et al.*, 2003). In contrast to the Baltic, a long-term decrease of diatoms in the North Sea has not been observed.

### Fish

Climate-mediated changes in copepod abundances affected major fish stocks in both the North Sea and the central Baltic Sea, but by very different mechanisms. In the central Baltic Sea, nauplii, copepodites, and adults of *A. longiremis* and *A. bifilosa* are the main food items of sprat larvae (Voss *et al.*, 2003). Consequently, it is assumed that the temperature-mediated increase of the *Acartia* spp. populations observed since 1988/1989 (Figure 8) contributed to the highly improved sprat recruitment since the late 1980s (Figures 9 and 10). Besides improved feeding conditions for larval sprat, higher temperatures also improve sprat egg survival (Köster *et al.*, 2003a, b). Thus, a chain of events leading from climate forcing to population increase of Baltic sprat can be constructed. The positive NAO index since the late 1980s led to a higher frequency of summer inflows of warm water into the central Baltic and, hence, to

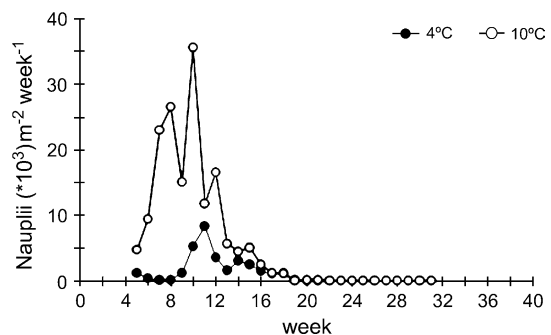


Figure 11. Hatching of *Acartia longiremis* nauplii from a sediment core under different temperature regimes.

increased temperatures of the IWW. Both processes favour hatching of copepod resting eggs in spring. Warmer temperatures also led to increased stratification in spring, favouring growth of dinoflagellates. Enhanced hatching of resting eggs and improved feeding conditions owing to the increase of dinoflagellates led to population increases of *Acartia* spp. and *T. longicornis* which, in turn, resulted in increases in the sprat population.

Interestingly, the climate-mediated population increase of sprat may have aggravated the decline of *Pseudocalanus* sp. by increasing predation pressure, thus displaying an indirect effect of the change in climate (Möllmann and Köster, 2002). The decline of cod, in turn, released predation pressure on sprat (Köster et al., 2001) and, in combination with high reproductive success attributable to favourable temperature conditions enhancing egg and larval survival, sprat reached exceptionally high stock sizes (Köster et al., 2003a, b). However, the rather long time-lag between the beginning of the cod stock decrease and the sprat stock increase (Figure 9) suggests that the absence of cod predation might be a prerequisite, but increased recruitment success is the primary cause of the observed sprat increase.

While the dramatic decrease of the central Baltic cod stock in the early 1980s (Figure 9) was caused by a combination of recruitment failure and concurrent overfishing (Köster et al., 2003b), the late 1980s regime shift might have contributed to the lack of the cod stock recovery. The most important food item of central Baltic larval cod, *Pseudocalanus* sp., shows very low abundance since the regime shift (Figure 8), mainly in response to lower salinities, not higher temperatures. However, the relatively low salinity of the central Baltic basins is believed to be a result of increased river run-off and the decreased frequency of winter saltwater intrusions from the North Sea, both of which might be related to the higher state of the NAO index since the late 1980s (Hänninen et al., 2000; Möllmann et al., 2003a).

In addition to the effects of overfishing, North Sea cod recruitment was negatively affected by higher temperatures associated with the high NAO index since the late 1980s. In the North Sea ecosystem, larval cod survival depends on the mean size, seasonal timing, and abundance of their prey. Abundance and mean size of the main larval food, calanoid copepods, have been at very low levels since 1987, and the progressive substitution of *C. finmarchicus* by *C. helgolandicus*, which occurred particularly after 1987, resulted increasingly in mismatch situations between larval cod and its *Calanus* prey as *C. helgolandicus* appears later in the year (Beaugrand et al., 2003). All of these major changes in the second half of the 1980s corroborate the hypothesis of a regime shift in the North Sea (Beaugrand et al., 2003).

In summary, major changes in three commercially important fish stocks, sprat and cod in the central Baltic Sea and North Sea cod, were brought about by bottom-up control resulting from a regime shift in the late 1980s. However, the mechanisms include complex physical as well as biological

processes leading to dramatic fish population changes, which were very different in all three fish populations.

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## References

- Alheit, J., and Niquen, M. 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography*, 60: 201–222.
- Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography*, 12: 270–283.
- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245–262.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661–664.
- Beaugrand, G., and Ibanez, F. 2002. Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. *Marine Ecology Progress Series*, 232: 197–211.
- Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9: 1–17.
- Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296: 1692–1694.
- Broglio, E., Jónasdóttir, S., Calbet, A., Jacobsen, H. H., and Saiz, E. 2003. Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquatic Microbial Ecology*, 31: 267–278.
- Chavez, F. P., Ryan, J., Lluch-Cota, S., and Niquen, M. 2003. From anchovies to sardines and back: multi-decadal change in the Pacific Ocean. *Science*, 299: 217–221.
- deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., and Shannon, L. 2004. Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography*, 60: 143–164.
- Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., Ottersen, G., Pershing, A. J., and Walker, H. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *In The North Atlantic Oscillation, Climatic Significance and Environmental Impact*, pp. 211–234. Ed. by J. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. *Geophysical Monograph*, 134.
- Dutz, J., Mohrholz, V., Peters, J., Renz, J., and Alheit, J. 2004. A strong impact of winter temperature on spring recruitment of a key copepod species in the Bornholm Basin: potential linkages to climate variability. *GLOBEC International Newsletter*, 10(1): 13–14.
- Edwards, M., Beaugrand, G., Reid, P. C., Rowden, A. A., and Jones, M. B. 2002. Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, 239: 1–10.
- Edwards, M., Reid, P. C., and Planque, B. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES Journal of Marine Science*, 58: 39–49.

- Feistel, R., Nausch, G., Mohrholz, V., Lysiak-Pastuszak, E., Seifert, T., Matthäus, W., Krüger, S., and Hansen, I. S. 2003. Warm waters of summer 2002 in the deep Baltic. *Oceanologia*, 45: 571–592.
- Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography*, 45: 703–710.
- Hansen, F., Möllmann, C., Schütz, U., and Hinrichsen, H-H. 2004. Spatio-temporal distribution of *Oithona similis* in the Bornholm Basin (central Baltic Sea). *Journal of Plankton Research*, 26: 659–668.
- Hare, S. R., and Mantua, N. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–145.
- Harrison, P. J., Turpin, D. H., Bienfang, P. K., and Davis, C. O. 1986. Sinking as a factor affecting phytoplankton species succession: the use of selective loss semi-continuous cultures. *Journal of Experimental Marine Biology and Ecology*, 99: 19–30.
- HELCOM. 1996. Third periodic assessment of the state of the marine environment of the Baltic Sea, 1989–93. *Baltic Sea Environment Proceedings*, 64B: 252 pp.
- HELCOM. 2002. Environment of the Baltic Sea area 1994–1998. *Baltic Sea Environment Proceedings*, 82B: 215 pp.
- Hinrichsen, H. H., Möllmann, C., Voss, R., Köster, F. W., and Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) survival and growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 1858–1873.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, 269: 676–679.
- Ianora, A., Miralto, A., Poulet, S. A., Carotenuto, Y., Buttino, I., Romano, R., Casotti, R., Pohnert, G., Wichard, T., Colucci-D'Amato, G., Terrazzano, G., and Smetacek, V. 2004. Aldehyde suppression of copepod recruitment in blooms of a ubiquitous planktonic diatom. *Nature*, 429: 403–407.
- ICES. 2002. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 2002/ACFM:17.
- Kleppel, G. S. 1993. On the diets of calanoid copepods. *Marine Ecology Progress Series*, 99: 183–195.
- Köster, F. W., Hinrichsen, H-H., Schnack, D., St. John, M. A., MacKenzie, B. R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Eero, A. 2003a. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. *Scientia Marina*, 67(Suppl. 1): 129–154.
- Köster, F. W., Möllmann, C., Neuenfeldt, S., St. John, M. A., Plikshs, M., and Voss, R. 2001. Developing Baltic cod recruitment models I: resolving spatial and temporal dynamics of spawning stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1516–1533.
- Köster, F. W., Möllmann, C., Neuenfeldt, S., Vinther, M., St. John, M. A., Tomkiewicz, J., Voss, R., Hinrichsen, H.H., MacKenzie, B., Kraus, G., and Schnack, D. 2003b. Fish stock development in the central Baltic Sea (1974–1999) in relation to variability in the environment. *ICES Marine Science Symposia*, 219: 294–306.
- Kröncke, I., Zeiss, B., and Rensig, C. 2001. Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. *Senckenbergiana Maritima*, 31: 65–82.
- Loewe, P., Becker, G., Brockmann, U., Frohse, A., Herklotz, K., Klein, H., and Schulz, A. 2003. Nordsee und Deutsche Bucht 2002 – Ozeanographischer Zustandsbericht. *Berichte des Bundesamtes für Seeschifffahrt und Hydrographie*, 33: 89 pp. (in German)
- Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2004. Feeding ecology of central Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). *Journal of Fish Biology*, 65: 1563–1581.
- Möllmann, C., Kornilovs, G., Fetter, M., Köster, F. W., and Hinrichsen, H-H. 2003a. The marine copepod *Pseudocalanus elongatus* as a mediator between climate variability and fisheries in the central Baltic Sea. *Fisheries Oceanography*, 12: 360–368.
- Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the central Baltic Sea. *Journal of Plankton Research*, 22: 2015–2038.
- Möllmann, C., and Köster, F. W. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the central Baltic Sea. *Journal of Plankton Research*, 24: 959–977.
- Möllmann, C., Köster, F. W., Kornilovs, G., and Sidrevics, L. 2003b. Interannual variability in population dynamics of calanoid copepods in the central Baltic Sea. *ICES Marine Science Symposia*, 219: 220–230.
- Reid, P. C., and Beaugrand, G. 2002. Interregional biological responses in the North Atlantic to hydrometeorological forcing. *In Large Marine Ecosystems of the North Atlantic*, pp. 27–48. Ed. by K. Sherman, and H. R. Skjoldal. Elsevier Science.
- Reid, P. C., and Edwards, M. 2001. Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima*, 31: 107–115.
- Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M., and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, 12: 260–269.
- Reid, P. C., Edwards, M., Hunt, H. G., and Warner, A. J. 1998a. Phytoplankton change in the North Atlantic. *Nature*, 391: 546.
- Reid, P. C., de Fatima Borges, M., and Svendsen, E. 2001a. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, 50: 163–171.
- Reid, P. C., Holliday, N. P., and Smyth, T. J. 2001b. Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. *Marine Ecology Progress Series*, 215: 283–287.
- Reid, P. C., Planque, B., and Edwards, M. 1998b. Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? *Fisheries Oceanography*, 7: 282–288.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K-S., and Lima, M. 2002. Ecological effects of climate fluctuations. *Science*, 297: 1292–1296.
- Voss, R., Köster, F. W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fisheries Research*, 63: 97–111.
- Wasmund, N., Nausch, G., and Matthäus, W. 1998. Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends. *Journal of Plankton Research*, 20: 1099–1117.
- Wasmund, N., and Uhlig, S. 2003. Phytoplankton trends in the Baltic Sea. *ICES Journal of Marine Science*, 60: 177–186.