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# Marine Ecosystems and Climate Variation

## The North Atlantic A Comparative Perspective

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# Effects of climate variability on benthic communities

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## 9.1 Introduction

Variability of population abundance is a typical feature of marine benthic communities at a variety of temporal and spatial scales (Cushing 1981; Botsford *et al.* 1982; Gray and Christie 1983; Baumgartner *et al.* 1992). Climatological factors are believed to be responsible for many aspects of temporal variability of marine communities (Aebischer *et al.* 1990; Francis and Hare 1994; Beamish *et al.* 1995; Stein and Lloret 1995; Ware 1995). The comparable role of periodic climatological variation in regulating physical and biological oceanographic processes in the North Atlantic region has been increasingly studied during recent years (see, e.g. earlier chapters in the book).

In order to elucidate the large-scale (oscillatory) climatological impacts on the benthic communities it has been necessary to analyse long-term benthic data from quantitative samples that have been collected at many sites on a regular basis over a large number of years (see, e.g. Chapter 1). Unfortunately, very few time-series are available that meet these terms. Recent shallow coastal benthic research has shown evidence of long-term periodicity in biotic communities, which appears to be associated with climatic periodicity (Kröncke *et al.* 1998; Tunberg and Nelson 1998). Tunberg and Nelson (1998) presented evidence for a periodic component in benthic community parameters and demonstrated that this periodicity is generally synchronized regardless of water depth. They also proposed that the periodic behaviour of benthic community processes is driven by a

periodicity on timescales similar to the periodicity of the North Atlantic Oscillation (NAO). This has been further confirmed by studies reported by Hagberg and Tunberg (2000).

A similar oscillatory pattern (7-year periods) has also been reported for the abundance of the benthic amphipod *Pontoporeia affinis* in the Bothnian Sea of the Baltic over the period 1961–74 (Gray and Christie 1983). Benthic foraminiferans have been studied in sediment cores from Gullmarsfjorden on the Swedish west coast and from the Skagerrak/Kattegat area. The foraminiferan community show a shift in the 1930s and in the 1970s in the Skagerrak (Alve 1996) and this shift has also been found in the Gullmar fjord between 1974 and 1976 (Nordberg *et al.* 2000). Both these shifts correspond to a shift in the NAO index from a predominantly positive phase to a negative phase in the 1930s and back to a more positive phase again in the late 1980s (Hurrell and Van Loon 1997; Nordberg *et al.* 2000). An interesting feature of these changes is that the fjord community of these foraminiferans exhibited a decrease of agglutinated foraminiferans, whereas in the open Skagerrak/Kattegat region they increased instead. Nordberg *et al.* (2000) suggested that the communities are affected by a factor connected to the NAO but that this factor has different effects in inshore and offshore areas.

Climatic variability is most likely to have an effect on marine populations and it is important to understand further the synchronicity between climatic oscillations and the life cycle of benthic species. In this chapter, we are summarising several

examples from different regions in order to illustrate these connections.

## 9.2 The North Sea

Several investigations in the Wadden Sea and coastal areas indicated that cold and mild winters affect macrofaunal communities (Ziegelmeier 1964; Zeiss and Kröncke 1997). Highly successful recruitment after cold winters results in increased biomass (Beukema 1990, 1992) indicating the importance of cold winters for the structure of littoral benthic communities (Beukema 1990, 1992; Reise 1993; Beukema *et al.* 1996). After a period of warm winters, Beukema (1990, 1992) found an increase in species number, stable total biomass, but a decrease in individual biomass of bivalves.

Off the island of Norderney sublittoral macrofaunal communities were severely affected by cold winters, but mild meteorological conditions during winter resulted in an increase in total biomass since 1989 (Kröncke *et al.* 1998). They showed that abundance, species number, and biomass in the second quarter of the year correlated with the NAO index. The mediator between the NAO and benthos is probably the sea surface temperature (SST) in late winter and early spring. Kröncke *et al.* (1998) explained this as a result of lower mortality and higher production and reproduction in mild winters in combination with an earlier spring bloom and possible synergistic effects between climate and eutrophication. According to the species composition off Norderney, Kröncke *et al.* (2001) found a higher percentage of arctic-boreal species after the cold winter of 1978/79 until 1982, and from 1984 to 1987 (a period with three rather cold winters and a negative NAO index) together with a rather high percentage of cold-temperate species. But after 1988 (in connection with a positive NAO index) the percentages of warm-temperate species increased.

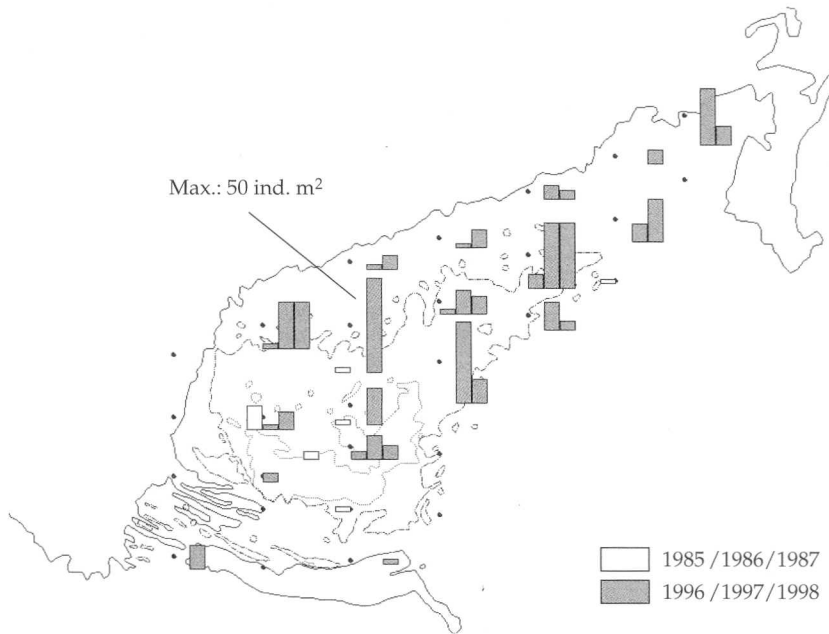
In the southern Bight of the North Sea the *Abra alba* community also showed a response to climate variability (Fromentin and Ibanez 1994). The analysis of a time series from 1977 to 1991 indicated that maxima of density always occurred during mild winters (1981–83, 1988–91) while very low densities of *A. alba* were concomitant with cold winters. That study confirmed that the *A. alba* time-series showed a periodicity of about 7.5 years corresponding to the same cycle of the air temperature pointing out the importance of the relation between the winter season and the fluctuations in the density of this

species. A similar cycle was also found by Glémarec (1993) in the interannual variability of benthic communities in Bretagne (France).

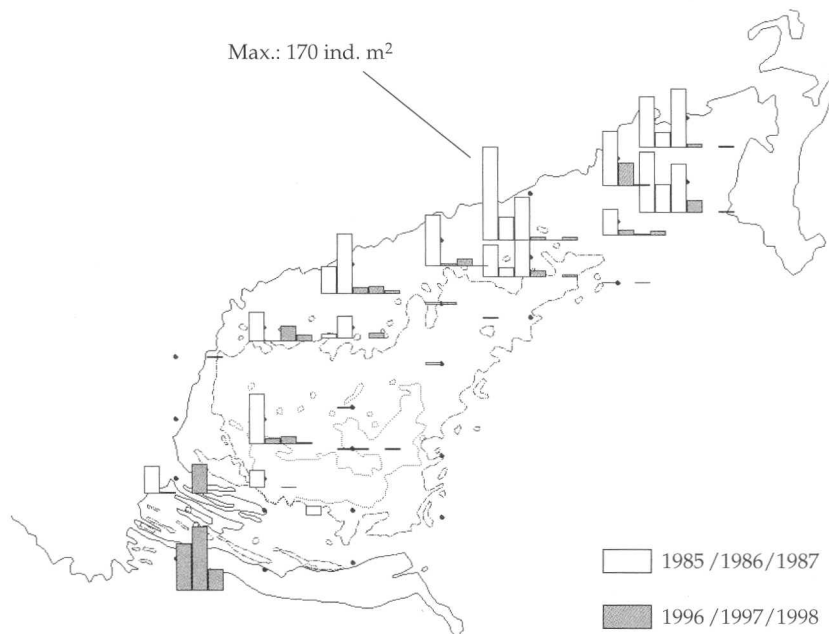
At a benthic station off Northumberland, Buchanan and Moore (1986) identified cold winters as an ephemeral destabilizing factor only. Cold winters favoured the survival in the dominant species at the expense of the lesser-ranked species due to reduced primary production. Most attempts of explaining the fluctuation in macrobenthos communities have been focused on factors that effect the food-availability (e.g. Rosenberg 1995). For example, the benthic fauna on the Northumberland coast showed a stable and repeating biennial pattern (Buchanan 1993). Food limitation was suggested to be responsible for this pattern. A high abundance in the spring resulted in a large number of competitively competent mature individuals. This resulted in few settled, less competitively, competent juveniles which lead to low abundances in the fall, and vice versa (Buchanan 1993). However, this pattern broke down in 1981 when abundances increased instead of decreasing, which was attributed to an increased food input to the benthos correlated with the intensity of inflow of Atlantic water masses into that area (Austen *et al.* 1991; Buchanan 1993). Strong connections between the inflow of North Atlantic Water to the North Sea and the NAO (Planque and Taylor 1998) suggest a possible relationship between the NAO and the Northumberland benthos.

In the frame of a long-term comparison between 1985–87 and 1996–98, Wiekling and Kröncke (2001) found marked changes in macrobenthic communities of the Dogger Bank (central North Sea) as a result of the rise in the NAO. Due to an increase in bottom temperatures southern species such as the amphipod *Megaluropus agilis* (Fig. 9.1) and the ophiurid *Amphiura brachiata* increased in abundance on top and at the southern slope of the Dogger Bank and occurred even in the deeper parts in 1996–98. In contrast abundances of northern species (e.g. *Corophium crassicornis*, *Siphonocoetes kroyeranus* [Amphipoda], *Nuculoma tenuis* [Bivalvia]) decreased on top and south of the Dogger Bank. The additional increase in abundances of interface-feeding species such as the polychaet *Spiophanes bombyx* coincided with a higher primary production in the central North Sea (Reid *et al.* 1998).

Benthic communities along the northern slope of the Dogger Bank were strongly affected by increasing wind stress and stronger currents at the northern



**Figure 9.1** Spatial distribution and abundance of *M. agilis* on the Dogger Bank in 1985–87 (white columns) and 1996–98 (dark columns) (from Wieking and Kröncke 2001).



**Figure 9.2** Spatial distribution and abundance of *O. borealis* on the Dogger Bank in 1985–87 (white columns) and 1996–98 (dark columns) (from Wieking and Kröncke 2001).

slope of the Dogger Bank. Factors which are also influenced by the positive NAO index during the 1990s (Siegismund and Schrum 2002; Siegismund 2001). Changes in larval supply, food availability, and sediment composition caused by resuspension of fine material lead to a decrease in species occurring on fine sand (*Ophelia borealis* [Polychaeta] Fig. 9.2) compared to the 1980s whereas abundances and total number of species preferring coarser and unstable sediment (e.g. *Echinocyamus pusillus* [Echinodermata]) increased in the 1990s. The decrease of total abundances, changes in trophic structure such as the increase in hyperbenthic predators (*Cerianthus lloydii* [Anthozoa], *Corymorpha nutans* [Hydrozoa]) and higher diversity of feeding types as well as the increase of total number of northern species were related to a stronger inflow of northern water masses and a connected decrease in food quantity and quality. These changes resulted in a pronounced separation of northern and southern macrofauna communities along the northern slope of the Dogger Bank during the positive NAO index period in the 1990s.

Pearson and Mannvik (1998) described an increase in detrital carbon supply to the benthos between 1993 and 1996 resulting in a considerable increase in macrobenthic faunal densities and species richness in the central North Sea, north of the Dogger Bank. They assumed that these changes are driven by climatic forces influencing the overlying water masses and some increase in pelagic productivity and benthic pelagic coupling. However, these observations are well in line with the NAO-driven increase in primary production in the Central North Sea.

With regard to the northern North Sea, Witbaard (1996) showed that year-to-year variation in the wind-driven component of the East Shetland Atlantic Inflow (ESAI) explains a significant part of the growth variations of the bivalve *Arctica islandica* from the Fladen Ground. Variations in the ESAI and the Dooley Current may influence the strength of the eddy system over the Fladen Ground and consequently the accumulation of material in its centre and the eddy mediated food-supply.

## 9.3 The Skagerrak and the Baltic Sea

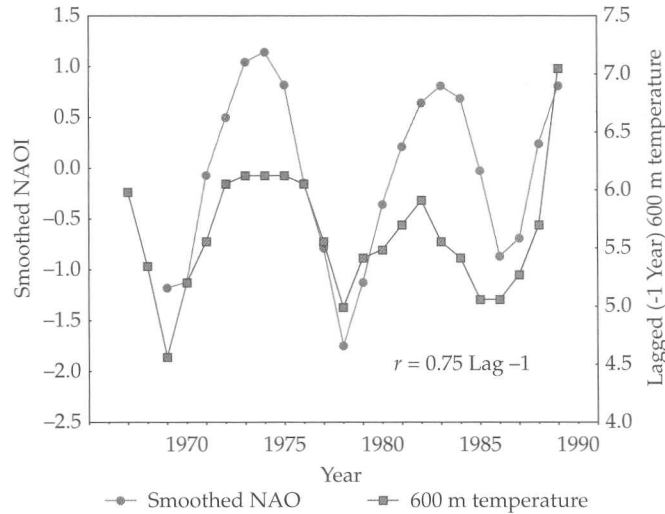
### 9.3.1 Skagerrak

The first indications of a linkage between the benthos and the NAO in the Skagerrak, were

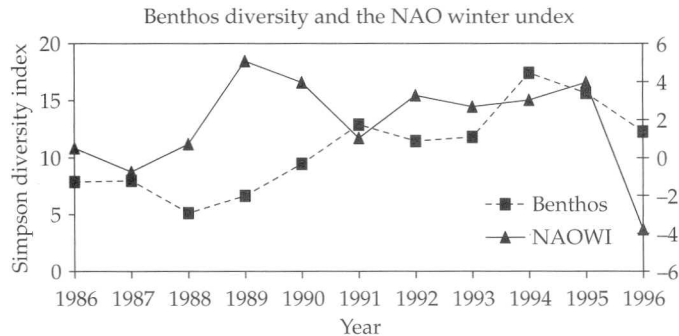
reported by Tunberg and Nelson (1998). They described a correlation between the macrobenthic soft bottom fauna and the NAO index, which indicated that the abundance and the biomass of the benthos generally decreased when the NAO index increased. Earlier studies reported a strong covariation of benthic abundances at different sites on the Swedish Skagerrak coast (Josefson 1987; Josefson *et al.* 1993). They suggested that land runoff was the key factor, driving this covariation. It was found that chlorophyll-*a* and dissolved inorganic nitrogen correlated positively with runoff and suggested that increased primary production, promoted by increased land runoff, increased the input of particulate organic nutrients to the benthos (Josefson *et al.* 1993). During this period the eutrophication debate was very intense and answers were sought primarily with this particular disturbance factor in mind.

Tunberg and Nelson (1998) found the same correlation between the benthos and land runoff as Josefson *et al.* (1993) found in the 1980s. They also concluded that the land runoff from the Swedish west coast correlated negatively to the NAO index ( $r = -0.57$ ). This may therefore explain the close correlation between the NAO index and the macrobenthic abundance. However, Tunberg and Nelson (1998) also found that the temperature at 600 m depth in the Skagerrak correlated positively to the NAO index (Fig. 9.3), but at a higher significance level than the land runoff ( $r = 0.75$ ). A possible explanation for this correlation has been given by Hagberg and Tunberg (2000) who suggested that the water exchanges of the Skagerrak deep water are driven by the NAO through the cooling of the North Sea surface water (see also Ljøen and Svansson 1972; Svansson 1975). Hagberg and Tunberg (2000) also concluded that the benthos in the Skagerrak correlated closer to the temperature at 600 m, than to runoff.

To illustrate further, some of the changes that occurred in the macrobenthos along the Swedish west coast we are using the data from station L4 at 40 m depth located at the entrance of the Gullmar fjord (58°14.68'N, 11°25.58'E). The Simpson diversity index (Simpson 1949; Magurran 1988) was calculated from the time series from 1986 to 96 and presented in relation to the NAO winter index. The results (Fig. 9.4) showed for the benthos an increase in diversity concomitant with the switch of the NAO in the late 1980s from a negative to a positive phase



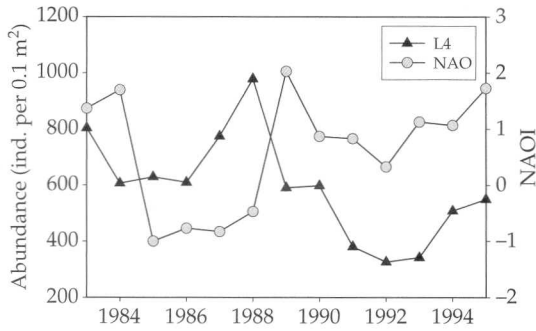
**Figure 9.3** Correlation between the temperature at 600 m depth in the Skagerrak and the NAO index (from Tunberg and Nelson 1998).



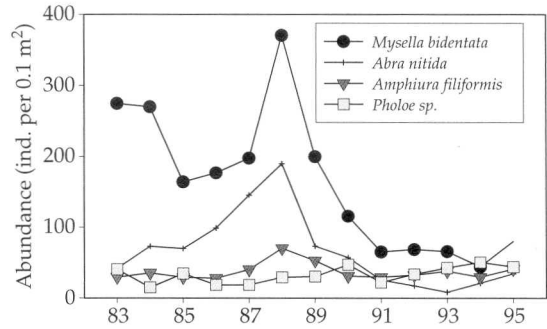
**Figure 9.4** Simpson diversity index 1986–96 presented in relation to the NAOWI (the winter-NAO index).

and this is indicated from the correlation coefficients ( $r = 0.12$ ;  $p < 0.05$ ). At this station the *A. alba* showed the highest density recorded in 1989 corresponding to a positive phase of the NAO and mild winter temperature thus reflecting a species-specific response to the NAO that was different compared with the changes in the total abundance at L4. This result confirms further the hypothesis of (Fromentin and Ibanez 1994) in relation to the density fluctuations in the *A. alba* in the southern Bight of the North Sea.

Data from site L4 also show a negative and significant correlation between changes in the NAO and benthic macrofaunal abundance (Fig. 9.5). As shown in the figure, abundance was lagging changes in the NAO significantly with 2–3 years. When combining benthic data from four sites between 18 and 40 m depth in the same area, a similar pattern was observed, with a significant time lag of 2 years ( $r = -0.86$ ) for the abundance. This indicates that the benthos generally increased ca. 2 years later than when the lowest NAO was



**Figure 9.5** Correlation between changes in the NAOWI and benthic macrofaunal abundance at site L4 off the Swedish west coast.



**Figure 9.6** Abundance pattern of the four most abundant species at site L4 during the period 1983–95.

recorded. Figure 9.6 shows the abundance pattern of the four most abundant species at site L4 during the period 1983–95, showing the occurrence of a peak in 1988 and a second increase in 1995, that is, ca. 7 years after an indication of the potential presence of a cycle.

The role of exogenous factors (Skagerrak deep-water temperature) and endogenous factors (competition, predation, and density dependence) in the Skagerrak macrobenthic communities was further studied by Hagberg *et al.* (2003), using autoregressive models. The results indicated very weak second-order interactions, suggesting that interspecific interactions did not affect the overall community dynamics very much. Also, the strong covariation of the Skagerrak deep-water temperature and total abundance could not be seen on single species abundance. The conclusions of these analyses were that the communities were loosely coupled entities, largely driven by large scale exogenous factors and that the composition is more of a random collection of species, although affected by local conditions.

### 9.3.2 The Baltic Sea

The highly enclosed Baltic Sea is eutrophicated (e.g. Cedervall and Elmgren 1980). This was demonstrated by comparing sampling results of macrofauna from 1923 with samples taken in 1976 and 1977. Cedervall and Elmgren (1980) were able to show an increase in biomass that could not be accounted for by either sampling methods or interannual variation. Brey (1986) showed a

similar increase in the macrozoobenthos between 1961 and 1965 and a study made in 1982–83. However, Andersin *et al.* (1978) found that the abundance of the amphipod *Pontoporeia affinis* showed a cyclicity of 7–8 years with clear peaks in 1966 and 1972. Low values were recorded in 1962 and 1969. There is also some evidence of a similar oscillation of *P. affinis* in the Gulf of Finland (Segerstråle 1969). Andersin *et al.* (1978) suggested intrinsic factors to be responsible for the observed cycles but they also found connections with the primary production changes in the Baltic. More recently Laine *et al.* (1997) studied changes in the macrofauna in the Eastern Gotland Basin and in the Gulf of Finland covering the period between 1965 and 1994. In this study, the major inflows of North Sea water during 1975–76 and 1993–94 led to highest oxygen condition in the 70–100 m depth zone as well as down to 250 m. This change in the hydrographical regime was followed by a recovery of the macrozoobenthos and recolonization in 1994 by polychaetes in the deepest part of the basin (243 m). These results pointed towards the importance of relating shifts in the hydrographical regime to changes in the climate and ultimately to the observed fluctuations in the macrobenthos. Salinity changes in the Baltic Sea have been regulated by the pulses of North Sea water entering via the Danish Straits and by the freshwater runoff. Hänninen *et al.* (2000) indicated that the NAO may be the forcing factor for a chain of events that regulate the inflow of more saline water to the Baltic as well the freshwater runoff with different lags. These results open up the possibility to make better and more accurate predictions concerning

oceanographic and biological interactions in the Baltic Sea.

#### **9.4 Outlook: comparison between the North Sea, the Skagerrak and the Baltic**

The major common feature in the different regions is the strong indication of a presence of a 7–8 year climate-driven cyclicity. This pattern has also been elucidated for the macrobenthos on the Swedish Skagerrak coast by Tunberg and Nelson (1998). They found that this cycle was synchronous with the NAO index but with a certain time lag. Since the NAO index also has been found to have a periodicity of 7–8 years (Rogers 1984; Tunberg and Nelson 1998), a possible explanation for the corresponding *P. affinis*

cyclicity in the Baltic could most likely be a close connection to the NAO. A possible explanation for this cyclicity (as suggested by Fromentin and Ibanez (1994)) could be the relation to the pole tide, which has a similar cycle (Gray and Christie 1983).

The variety of studies indicate that single species as well as whole communities and also functional groups are influenced by changes in the NAO, and dependent on the species composition of the different communities the impact also may differ geographically.

A modelling study by Paeth and Hense (1999) suggests that the NAO is likely to remain positive for the next four decades. We may therefore expect major changes in the benthic communities of the North Sea and the Baltic Sea.