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A statistical analysis of climate variability and ecosystem response in the German Bight

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Abstract We compiled homogeneous long-term time series comprising 39 variables representing the German Bight and for the period 1975–2004. A diverse set of variables was selected to cover multiple trophic levels and different environmental forcing thus to examine long-term changes in this coastal region. Previous studies have hypothesised the presence of regime shifts in observations extending over the entire North Sea. Focusing on a smaller spatial scale, and closer to the coast, we investigated the major modes of variability in the compiled time series using principal component analysis. The results obtained confirm a previously identified regime shift in the North Sea in 1987/1988 and suggest that the German Bight is dominantly characterised by long-term modes of variability. In the German Bight, the shift of 1987/1988 is driven primarily by temperature, Gulf Stream index, frost days and Secchi depth. Changes in some of the ecosystem variables (plankton and fish) appear to be related to changes in these driving variables. In particular, we documented strong positive correlations between the long-term trend showed by the first principal component and herring, *Noctiluca scintillans*, and, to a lesser extent, *Pleurobrachia pileus*. Two gadoids, namely cod and saithe, showed negative correlations with the observed long-term mode of variability. Changes in the sum of five small calanoid copepods were, however, less marked. Phosphate and ammonium exhibited a decreasing trend over the last 30 years. Diatoms and *Calanus helgolandicus* did not show evidence of changes in concert to this trend. Specific analyses of the data divided into three different subsets (biological, climatic and chemical) characterise the climate of the German Bight as highly dynamic also on short timescales (a few years) as compared to much smoother biological and chemical components. The dynamic regime of the German Bight taken together with a low correlation between the major mode of variability and phytoplankton and zooplankton data suggests that the lower trophic levels of this ecosystem are remarkably resilient.

Keywords Climate change, German Bight, Principal component analysis, Marine ecosystem, Long-term trend, Helgoland Roads

Introduction

Global climate change is likely to affect the physical and biogeochemical characteristics of the oceanic and coastal environments with potentially profound impacts on ecosystems (IPCC 2007). The analyses of long-term time series can help to understand how ecosystems respond to climate variability and to evaluate potential effects of anthropogenic perturbations.

In the North Sea, interannual and interdecadal variability has been observed in both hydrographical and biological variables. One of the strongest interdecadal signals, known as the Russell cycle (Russell 1973), was detected during the late 1920s and was characterised by a shift in the plankton community structure of the English Channel. The Russell cycle reversed during the late 1960s (Russell 1973). Another important mode of variability, consisting in a body of water with very low salinity and temperature entering the North Sea, was detected by Dickson et al. (1988) and was called the great salinity anomaly (GSA). Although it has been proposed (Cushing 1988) that the GSA event adversely affected the recruitment of a number of deep water fish stocks through a delay of the phytoplankton spring bloom, Mertz and Myers (1994) expressed doubts on the strength of such a climate–food web coupling.

In data collected in the western North Sea by a continuous plankton recorder (CPR), Reid (1975) observed a marked decrease in diatom abundance after 1965. Since the CPR data also suggested that at the same time the relative estimate of phytoplankton standing crop increased, Reid concluded that a shift in species composition must have been taking place in this area in 1965 with a consequent impact on higher trophic levels. Aebischer et al. (1990) reported of remarkable similarities in trends among abundances of phytoplankton, zooplankton and herring, kittiwake gull breeding performance and variations in westerly weather. Although, as Aebischer et al. (1990) admitted, the reasons for these similarities remain unclear, it is tempting to call for a straight causal relationship between weather and ecosystem shifts.

More recently, Dippner (1997a, b) suggested that coastal areas of the North Sea could be very sensitive to climate change. The author supports the hypothesis that the coastal areas are mainly driven by direct atmospheric forcing rather than, for instance, by inflow of Atlantic water (Cushing 1988, 1990).

More relevant to our study, Heyen and Dippner (1998) proposed that in the German Bight, the interannual and interdecadal variability in surface salinity is correlated to river runoff rather than advection of Atlantic water. For the same area, Kröncke et al. (1998) found that the biomass, abundance and species number of macrozoobenthos is strongly affected by climate variability.

In addition to these signals, two dynamic regimes in the North Sea plankton ecosystem were found: a cold biological (1962–1982) regime and a warm biological (1984–1999) regime (Beaugrand and Ibanez 2004). In addition, Beaugrand (2004) and Edwards and Richardson (2004) proposed that a regime shift covering the period 1982–1988 in the North Sea may be connected to changes in largescale hydrometeorological forcing. A similar ecosystem response to climate variability has been previously detected in the Pacific Ocean by Hare and Mantua (2000). Beaugrand et al. (2002a) recognised large biogeographical shifts in all copepod assemblages in

the eastern North Atlantic Ocean and European shelf seas in the early 1980s. Beaugrand et al. (2002b) demonstrated that warm water North Atlantic species moved further towards north, in association with a decrease in the number of cold water species, in relation to an increasing trend in the Northern Hemispheric temperature and North Atlantic Oscillation (NAO). Reid et al. (2001) reported an ecological regime shift in the North Sea around 1988 based on a compilation of plankton data derived from the CPR and fish catchments. Such regime shift was clearly detected in the northern and central North Sea, but not in the southern North Sea (Beaugrand and Ibanez 2004). An important result of these studies is that with increasing temperature, a shift occurs in the species composition from cold to warm water adapted species. Weijerman et al. (2005) investigated the possibility of a connection between physical changes and ecosystem state in the North and Wadden Seas. The authors suggested that regime shifts occurred in 1979, 1988 and 1998, although results were less clear-cut in the latter case. More recently, also Kirby et al. (2007) documented some climatic impacts on the North Sea ecosystem. McQuatters-Gollop et al. (2007) showed that chlorophyll a (Chl a) increased from the mid-1980s with a regime shift peak in 1989 to higher concentrations in both the open and the coastal North Sea. The authors suggest that the North Sea phytoplankton biomass is unconnected to nutrient trends but positively correlated with Secchi depth and sea surface temperature (SST).

We compiled a homogeneous long-term time series of data for a limited part of the southern North Sea: the German Bight. The resulting dataset includes 39 different variables and spans over 30 years. By using principal component analysis (PCA), we investigated the dominant modes of variability in the dataset and identified the variables most accountable for those modes. In particular, we addressed the following questions:

1. Can we identify regime shifts in the German Bight?
2. What is the timescale of these events?
3. What are the variables dominating these events?
4. Can causes and effects be clearly identified?

Alternatively to many other studies of this kind, we focus on a restricted location of the southern North Sea: the German Bight. We provide for the first time a detailed understanding of climate variability in this region, not based on physical and biological data only but also on chemical variables. However, our results will be discussed also in the context of the overall North Sea variability.

Materials and methods

In order to identify basic structures of variations, which reflect more clearly the influence of an external forcing, we compiled a diverse set of data including multiple trophic levels and several physical and chemical variables for the German Bight (6°30 E to 9°10 E and 53°30 N to 55°10 N, see Fig. 1 for a map of the region).

Unbiased observations of nature are almost impossible; thus, we selected data with the following criteria: (1) the time series had to be homogeneous, no obvious anthropogenic cause for sudden changes in the time series and no or few missing values in the dataset; (2) long-term diverse set of variables including multiple trophic levels and different environmental indicators and (3) different sites representative of the German Bight. The resulting dataset comprises a total of 39 variables spanning over 30 years and divided into three major categories: atmospheric and

hydrophysical variables (19), biological variables (14) and chemical variables (6); see Appendices 1 and 2 for a full list of variables and descriptions. The biological variables were log-normalised and all time series were normalised by calculating the anomalies (deviations from the mean for each data point) and dividing these by the standard deviations. No smoothing or filtering techniques were applied to the data.

Following the approach of Hare and Mantua (2000), we used PCA for our investigation. PCA has been used in many studies to objectively identify coherent patterns of variability among a number of time series (Mantua 2004). In brief, the PCA is an “ordination technique” that reduces the dimensionality and identifies the most important modes of joint variability in a multivariable dataset. Assuming that the data are linearly related, the PCA defines an orthogonal linear transformation that transforms the data to a new coordinate system such that the greatest variance by any projection comes to lie on the first coordinate (the first principal component), the second greatest variance on the second coordinate (the second principal component) and so on. This way, one can capture the most important fluctuations in the data with a few components.

A PCA generates three types of outputs: principal components (PCs), eigenvectors (or loadings) and eigenvalues. When plotted against time, PCs give the temporal variability of the most dominant patterns. Eigenvectors indicate which variable contributes most to the dominant patterns. Eigenvalues are used to determine the fraction of total data variance explained by each PC.

For a detailed review of the PCA method, see von Storch and Zwiers (1999). Once we computed the first principal component, we quantified the overall step magnitude of the regime shift using the method of Ebbesmeyer et al. (1991).

For investigating correlations between subsets of time series, we used canonical correlation analysis (CCA). As with PCA, there may be more than one significant dimension (more than one canonical correlation), each representing an orthogonally separate pattern of relationships between the two subsets of variables. The first canonical correlation is always the one that explains most of the relationship. The canonical correlations are interpreted the same as Pearson's r .

Although the term “regime shift” is widely used in the literature, there is no universal definition for it. Lees et al. (2006) reviewed different criteria used to define a regime shift. Typically, common characteristics like speed and amplitude of the changes and the duration of quasi-stable states are used for defining climatic and ecological regime shifts. Lees et al. (2006) suggested that a standard definition should meet a number of conditions (like sudden, highamplitude, infrequent events, number of trophic levels impacted by the shift and biophysical impacts) before a change in the data can be classified as a regime shift. Arguably, it is difficult to assess how useful these criteria are in universally characterising regime shifts.

We are interested in shifts that are not smooth or reversible within a short period (1 or 2 years). Therefore, we adopted the following definitions:

Regime = Quasi-stationary state of a system persisting for several years and characterised by low-frequency variability.

Regime shift = Transition period between two regimes that occurs within a year or two.

To prove the robustness of the results, we performed PCA with longer and shorter time series. Because the zooplankton time series did not start before 1975, by excluding zooplankton, we conducted PCA on longer time series starting from 1966 and up to 2004. Due to the expected

regime shift in the late 1980s, we also performed PCA starting from 1983 so to examine this signal in more detail.

Results

We used principal component analysis to reduce our dataset to new, fewer variables, called “principal components” (PCs), which account for the majority of the variability in the data. Eigenvalue analysis (see Fig. 2) indicates that the first principal component (PC1) describes the dominant mode of variability in our dataset. The first and second principal components account for 23% and 12% of the total variance, respectively (note that the percentage of variability explained by the first principal component is far above the equiprobability value= $1/33=3.03\%$). Since the interpretation of PCs higher than the first is problematic because they are constrained to be orthogonal to each other and natural processes are not necessarily independent from each other (von Storch and Zwiers 1999), we decided to focus our study on the first PC only.

Figure 3 shows the temporal variation of PC1. The loadings (correlation coefficients between each time series and PC1) are illustrated in Fig. 4. According to our definition, the temporal evolution of PC1 shows a pattern with two regimes: negative until 1987 and then positive thereafter, with an abrupt shift in 1987/1988. The year 1996 appears to be anomalous in that PC1 is temporarily reversed in sign. The PC1 shows a minimum in 1979 and a maximum in 2002. Among the environmental variables, air temperature, SST, winter SST and Gulf Stream index show the strongest positive correlation with PC1 (see Fig. 4). In addition, Secchi depth is positively correlated with PC1. High negative loadings are found in nutrients like phosphate (PO₄) and ammonium (NH₄). Cod and saithe show high negative correlation with PC1, whilst herring shows high positive correlation with PC1. In agreement with an increasing warming trend (Edwards et al. 2002; Edwards and Richardson 2004), frost days show high negative correlation with PC1. Temperature, through its influence on physiological processes, can potentially affect ecosystems (Kirby et al. 2007). However, not all biological/ecosystem variables showed pronounced shifts in our analyses. Diatoms and *Calanus helgolandicus*, for instance, did not show high correlation with the PC1, although other zooplankton species (sum of five small calanoid copepods, *Noctiluca scintillans* and *Pleurobrachia pileus*) showed slightly higher correlations (Fig. 4).

Note that the way we use the PCA does not imply that all 33 variables (or the majority of them) should show the same pattern as PC1. In other words, with the PCA we have determined, a significant subspace (in terms of number of variables) in which the change shown in PC1 is observed.

To quantify the overall step magnitude of the regime shift, we used the method of Ebbesmeyer et al. (1991). Figure 5 shows the step magnitude in the temporal evolution of PC1 as given by the difference between the two regimes (red dashed line in Fig. 5). The marked stepwise increase in 1987 is about one standard deviation high. Figure 5 also shows that the two regimes are characterised by rather small interannual variations.

To statistically test the (in)equality of the means (before and after the shift) of the two identified regimes, we used the Student’s *t* test. The null hypothesis is that the variables are normally distributed with the same variance and that the samples are randomly independent with equal means. The alternative hypothesis is that the means are not equal. The test of (in)equality of means is performed by applying a two-tailed *t* test. The result suggests the rejection of the null hypothesis at the 5% significance level.

However, some data violate the assumptions of the *t* test. Therefore, we also used the Mann–Whitney *U* test for testing the (in)equality of the two medians. Furthermore, in this alternative

approach, the result suggests the rejection of the null hypothesis of equal medians at the 5% significance level.

To quantitatively ascertain that the two regimes (before and after the shift) are different, we used a resampling bootstrap test on the means of the two regimes. This technique involves choosing random samples with replacement from our dataset and analysing each sample the same way with the PCA. A confidence interval for the difference of the means of each regime is calculated from the constructed synthetic time series. This exercise is repeated 1,000 times. The null hypothesis is rejected at the 5% significance level, indicating that the two means are well separated.

Following Mantua (2004), in order to identify dominant ecosystem state variables and to better isolate ecosystem behaviour from other influences (like environmental changes), we separated the data into three categories: (1) biological, (2) climatic and (3) chemical. In Fig. 6, we show the results of PCA performed on each of these groups. The first PC of the chemical data (see Fig. 6a) explains 32% of the total variance. Note that the second regime of the first PC for chemical data is not as smooth as the second regime in the PC1 obtained with the global dataset (Fig. 3). Ammonium (NH₄) and phosphate (PO₄) show the strongest negative correlation with the first PC of chemical data, whilst salinity shows the strongest positive correlation with the first PC of chemical data. This may be connected to the fact that the German Bight waters changed over the last decade from a more coastal (fresher)-dominated character to a more marine-dominated character (clearer and saltier; see Beare et al. 2002; Wiltshire and Manly 2004).

The first PC of climatic data (Fig. 6b) shows pronounced interannual variability (likely reflecting the fact that physical variables respond faster to atmospheric changes and characterising the German Bight climate as highly dynamic) and has a distinct peak in 1996. The variance explained is 35%. The highest loadings are given by the temperature data similarly to the results obtained with the global dataset (Fig. 3), and accordingly, the highest negative correlation with the first PC of climatic data is mainly given by frost days.

Figure 6c shows the results of the PCA performed on the biological data. The first PC of biological data explains 25% of the total variance and is the smoothest among the three first PCs. Fish data such as (saithe, cod and to a less extent haddock) show high negative correlation with the first PC of biological data and positive for herring similar to the results obtained with the entire dataset. *N. scintillans* show high correlation with the first PC of biological data as well as *P. pileus*.

In summary, the first PC obtained on the global dataset shows a regime shift in 1987/1988. The first PCs of chemical, climatic and biological time series are dissimilar from each other, highlighting the different modes of variability expressed by the three different categories of data and suggesting that the biological component of the German Bight system is rather resilient.

Regime shift analysis

We performed an analysis of similarity test (ANOSIM) of the two regimes (before and after the shift). The statistical significant difference obtained was $R=0.82$, suggesting that the two regimes are indeed well separated and clearly distinct. The estimated probability that such a result could be generated by random chance is $p=0.001$. We used 1,000 permutations for estimating the significance level R .

To further investigate our results, we plotted the first PC of all biogeochemical data against the first PC of all hydrophysical data (Fig. 7). Two clusters show up with a separation in 1987. This year marks a tipping point around which the system shifts into a new state.

The year 1996 is confirmed to be anomalous in that the changes occurred did not force the system to shift into a contrasting permanent regime. We also performed CCA to study the relationship between biogeochemical and hydrophysical data. This statistical technique identifies the maximised correlation between two datasets. For both datasets, the canonical correlation was $r=0.9$.

Discussion

The impact of a changing climate on marine ecosystems is generating a wealth of new investigations. In this context, we think it is important to investigate whether the regime shifts suggested by various studies in the North Sea have also taken place locally, especially for highly populated coastal areas such as the German Bight.

In general, our results obtained by focusing on the German Bight and by including new time series confirm those of earlier studies targeting the entire North Sea (Reid et al. 2001; Beaugrand 2004; Beaugrand and Ibanez 2004; Weijerman et al. 2005): A regime shift took place in 1987/1988 with important ecological consequences.

The underlying mechanisms for the shift can be inferred by analysing the SST data in more detail. Figure 8 shows the SST averaged over winter (Jan–Mar) and the SST averaged over summer (Jul–Sep). There were two exceptionally cold winter years (1979 and 1996) and an event of persistent cold winters from 1985 to 1987. The extreme cold anomaly of North Sea SSTs in 1996 is correlated with a persistent negative phase of the North Atlantic Oscillation (Loewe 1996). The regime shift of 1987 is also preceded by persistent cold summers (from 1984).

We suggest that the repeated cold events observed in summer and winter SST might have been responsible for the shift shown in variables of higher trophic levels through the impact of persistent lower temperatures on physiological processes.

The increasing warming trend (Fig. A2.8), which has been attributed to global warming (Edwards et al. 2002; Edwards and Richardson 2004), might explain the persistence of the second regime shown by our analysis.

Our analyses also suggest that temperature is an important player in the regime dynamic of the German Bight ecosystem. Plankton dynamics is indeed strongly influenced by temperature (Beaugrand and Ibanez 2004; Dippner 1997a; Fromentin and Planque 1996; Planque and Fromentin 1996; Kröncke et al. 1998). Temperature may influence trophic interactions in several ways: (1) it determines the geographical distribution of many species, and (2) it affects physiological factors such as etching of eggs, respiration, growth, etc. Ecosystems may therefore be expected to show clear responses to a warming climate.

For instance, we obtained negative anomalies in North Sea cod spawning stock biomass (SSB) and this was correlated with a positive temperature anomaly. We can think of two possible factors that could account for a decrease in cod SSB: (1) a higher mortality in juvenile fish, resulting from a reduction in food supply (a bottom-up effect proposed by Russel 1973), or (2) a northward move of adult fish populations towards regions where temperatures are more favourable (Svendsen et al. 1995). It is more likely that the decrease in the number of cods is due to this northward shift given that cods are adapted to colder temperatures (Svendsen et al. 1995). Dippner (1997b) also put forward the possibility of recruitment failure in North Sea cod, North Sea whiting and western mackerel in association with a warming climate. In our analysis, negative anomalies in North Sea saithe SSB are correlated with positive temperature anomalies, suggesting that the recruitment success of this fish is connected with warm temperatures. This is

in agreement with the study of Svendsen et al. (1995) indicating a positive response of North Sea saithe recruitment to warmer water. We obtained positive anomalies in herring SSB. A possible explanation might be that herrings had an extended reproductive phase from 1990 to 1996, possibly due to the location of several sites within or near Helgoland exhibiting different spawning times (Greve et al. 2005).

Note that our SSB data cover year classes of 0–1 year, thus excluding the possibility of lags between SSB data and hydrometeorological forcing (Dippner and Ottersen 2001; Sundby et al. 1989; Helle et al. 2000).

Note that in our PC analysis, we did not take into account any lag between Gulf Stream index (GSI) and other climatic variables because of the contrasting results existing on these points (see for example Frankignoul and de Coetlogon 2001). Joyce et al. (2000) found that the correlation with the North Atlantic Oscillation (NAO) during winter was best at zero lag or Gulf Stream lagging by 1 year. They argued that the unlagged correlation may reflect a response of the NAO to the Gulf Stream shifts.

In the case of zooplankton, our results show positive correlations of the abundance of *N. scintillans* and *P. pileus* with PC1. Heyen et al. (1998) detected that a warm North Sea (in late winter) coincides with high abundance of *N. scintillans*. They concluded that evidence exists that high water temperature in winter leads to an earlier start of the growth season of *P. pileus* and to earlier timing and high abundance of *N. scintillans*.

Beare et al. (2002) maintains that winters (January, February) have become considerably warmer than in the late 1960s. Beare et al. (2002) found that the *Calanus finmarchicus* population of the North Sea collapsed in the late 1950s, whilst abundance of temperate Atlantic species like *C. helgolandicus* and neritic species increased. The authors suggest that the fall in the population of *C. finmarchicus* coincided with long-term freshening and warming of the western North Sea and a long-term increase in the salinity of the eastern North Sea. Fromentin and Planque (1996) showed that the increase in temperature and alteration in the winter circulation pattern observed during the last decades of predominantly positive NAO index values have proven beneficial to *C. helgolandicus*, the abundance of which has increased. However, our result for *C. helgolandicus* differs from the findings just described and did not show high correlation with PC1. For our analysis, time series of *C. helgolandicus* are collected at the Helgoland Roads (HR) station. A possible explanation for the discrepancy might be that *C. helgolandicus* at Helgoland Roads are subject to higher predation and lower water depths in contrast to the North Sea. At Helgoland Roads, Greve (2003) showed that the annual dynamics of *C. helgolandicus* changed in the 1990s compared to the 1980s due to the change in annual dynamics of *P. pileus*. *P. pileus* and *C. helgolandicus* prey on each other at appropriate developmental sizes. This interaction can thereby determine their relative dominance within the ecosystem (Greve 1995). They are mutually exclusive, and higher abundances of *P. pileus* can be the driver of a later growth of *C. helgolandicus*.

Beaugrand et al. (2002a) demonstrated that clear biogeographical shifts in most of copepod assemblages have occurred with a northward extension of warm water species associated with a decrease in the number of colder water species. These biogeographical shifts were related both to the increasing trend in Northern Hemisphere temperature and to the North Atlantic Oscillation. In our case, we found that small calanoid copepods are negatively correlated with annual temperature. In other words, whilst the temperature anomaly is positive in the second regime (Fig. A2.7), the small calanoid copepods abundance is lower in this period (Fig. A2.3). We suggest that phytoplankton–zooplankton mismatches might be responsible for this patterns through warmer winter temperature (Fig. A2.8), causing an earlier zooplankton development. However, we cannot rule out the possibility of a top-down control via predation. Greve (1994)

documented an exceptional invasion of a population of *Muggiaea atlantica* in the German Bight in 1989, increasing the grazing pressure on small copepods.

Our result in the case of diatoms shows weak correlation with the first PC. Diatoms are unicellular short-lived phytoplankton and are subject to predation and to other processes affecting their physiology. Their population may increase exponentially and double within a few days. The low correlation with the increase of long-term SST might indicate that the long-term trend in SST is not a first-order influence on diatoms, rather other factors as the amount of incident light and temperature variability in the beginning of the year might determine their variability (Wiltshire et al. 2008). We do not exclude the possibility that more than one mechanism may be responsible for the patterns observed, thus leading to complex nonlinear relationships between climate variability and diatom populations. In addition, after 1987/1988, the regime shift of the mean diatom day (MDD) did not change. This is in line with the recent work of Wiltshire et al. (2008) who found fairly stable spring bloom timings at Helgoland Roads.

The long-term trend of the HR ammonium time series reflects its overall “true” variability in the southern North Sea (see also Raabe and Wiltshire 2008). For instance, ammonium concentration at HR shows a similar trend (a decrease) to the Dutch coastal waters (Schaub and Gieskes 1991). Ammonium loads from the Elbe river have also been decreased since the 1980s (Hickel et al. 1993 and 1995), consistently with observations at HR. A relation between Elbe River and nutrient concentrations at HR has been established since a long time now (Lucht and Gillbricht 1978).

Generally speaking, a reliable Secchi depth dataset should be positively correlated with salinity (Hakanson and Blenckner 2008). Our data reflect this relationship: the higher the salinity, the clearer the water. A recent study by McQuatters-Gollop et al. (2007) showed that water transparency, based on Secchi depth data, has been increasing in the coastal North Sea waters after a major decline during the early 1970s. The trend shown in our Secchi depth data is consistent with the work of McQuatters-Gollop et al. (2007; Fig. A2.9).

Summary and conclusions

We compiled a diverse set of long-term time series for the German Bight. The resulting dataset contained variables representing atmospheric, hydrophysical, biological and chemical observations. We used PCA to identify the most important modes of variability in the data and determined the variables with highest correlation to these modes and used a number of tests for supporting the robustness of our results. This approach allowed us to tackle some important scientific questions (as listed in “Section 1”). Our answers are as follows:

1. Our analysis indicates that the major mode of variability in the data is characterised by two regimes separated by an abrupt shift in 1987/1988 (first PC).
2. The two regimes persist for more than a decade (although we cannot provide evidence for the state of the system before 1975 and after 2004). The regime shift takes place in within a year and is statistically significant.
3. We found that SST, air temperature, SST winter and herring showed the highest positive correlation to the major mode of variability (first PC), whilst phosphate, ammonium and some fish (cod and saithe) showed the highest negative correlation with the first PC. A pronounced positive correlation was also found for the Gulf Stream index, Secchi depth and salinity.

Consistently with an increasing warming trend, frost days showed high negative correlation with the first PC.

4. High positive loadings in SST, Gulf Stream index and Secchi depth (and to some extent also in salinity) suggest that the regime shift of 1987/1988 in the German Bight is likely caused by changes in these variables. This conclusion is also supported by previous studies (Beare et al. 2002; Wiltshire and Manly 2004) maintaining that in the last decade, the German Bight has been characterised by clearer and more marine waters. Changes in some ecosystem variables (plankton and fish) are associated to changes in the hydroclimatic forcing. However, not all biological variables showed pronounced shifts. Diatoms and *C. helgolandicus*, for instance, did not show high correlation with the major mode of variability (first PC), suggesting that the lower trophic levels of the German Bight ecosystem are remarkably resilient. In fact, specific analyses of the data divided into three different subsets (biological, climatic and chemical) characterise the climate of the German Bight as highly dynamic also on short timescales (a few years) as compared to much smoother biological and chemical components.

Our study documented for the first time that the German Bight is characterised by patterns of variability similar to the ones of the all North Sea (Beaugrand 2004; Weijerman et al. 2005). The German Bight, however, is characterised by a different exposure to natural and anthropogenic perturbations with respect to the all North Sea. In our analysis, we included various nutrients and we showed that phosphate and ammonium are characterised by stronger negative trends with respect to the weaker positive trends in silicate and nitrate concentrations. Although this coastal region appears to be characterised by a quite dynamic climate regime, lower trophic levels of the ecosystem appear to be rather resilient.

Given the complexity inherent to the studies of coastal ecosystem variability, it is crucial that long-term monitoring programmes are maintained in the future and that combined statistical analysis and ecosystem modelling approaches are undertaken.

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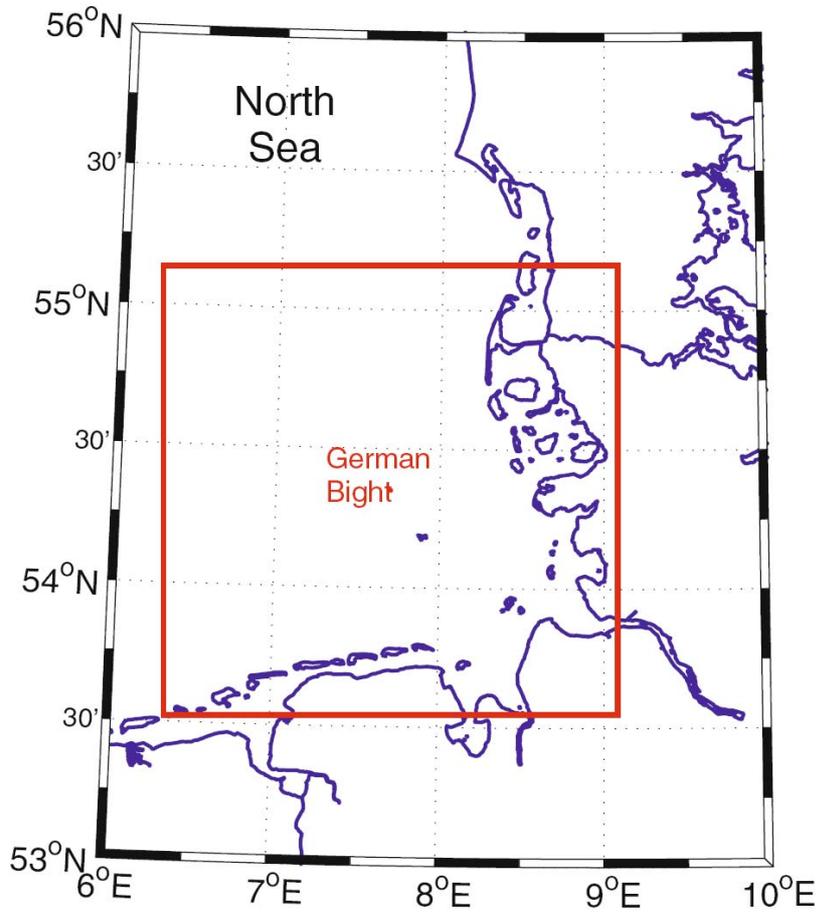


Fig. 1 Map of the North Sea and the area of the German Bight for analysis enclosed in the red box

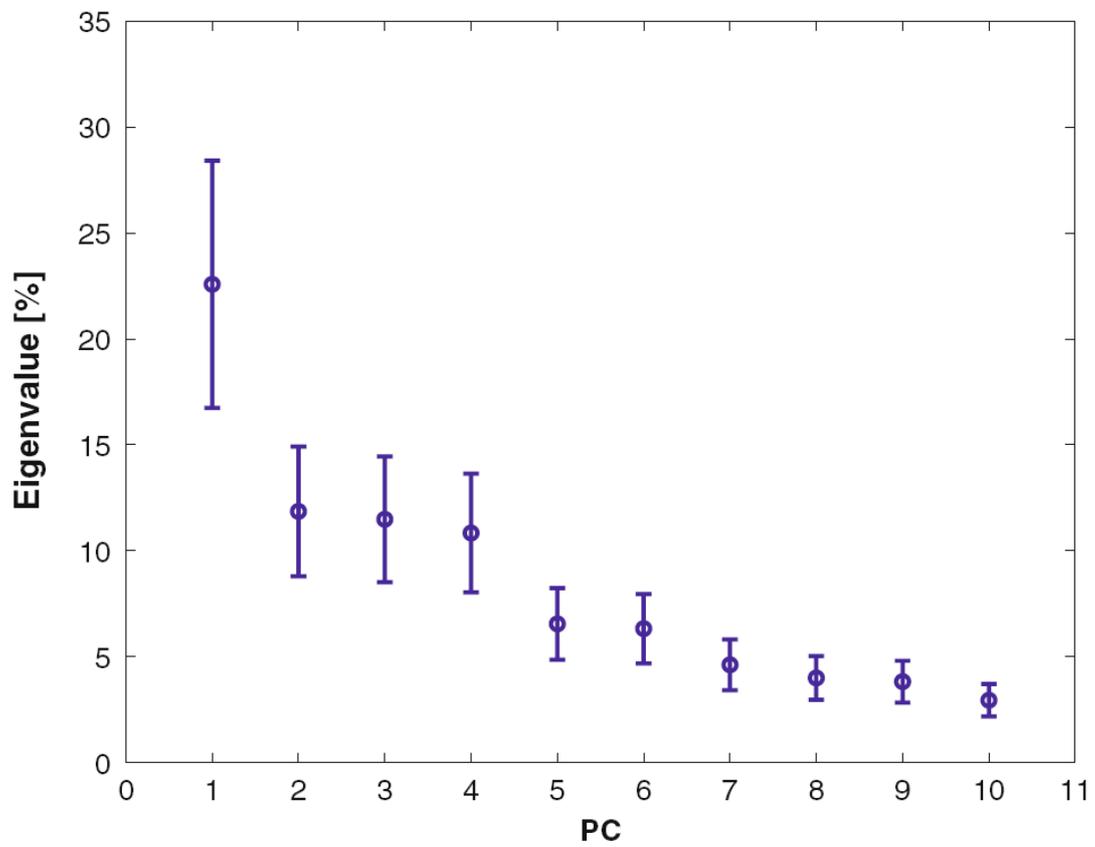


Fig. 2 Scree plot of the first ten eigenvalues for the principal component analysis of the full set of variables and their estimated standard errors

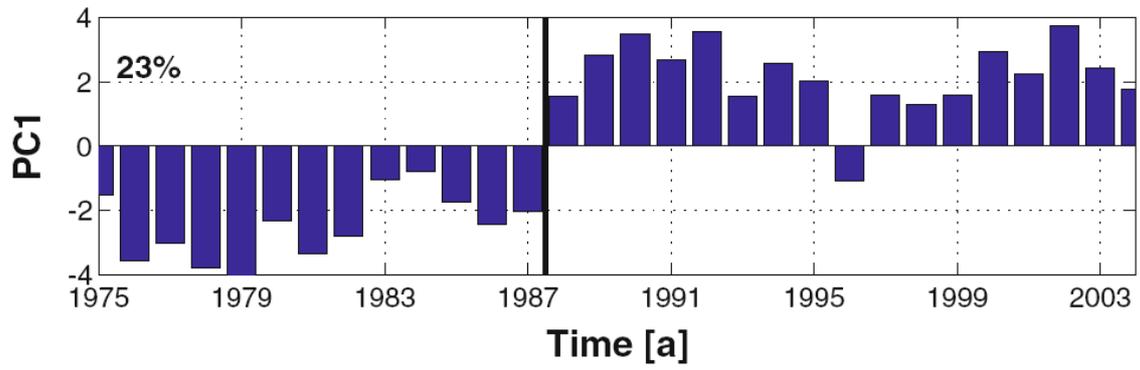


Fig. 3 The first principal component (PC1) of the principal component analysis of the full set of variables for the time period from 1975 to 2004. The black vertical bar is shown before the data point 1988

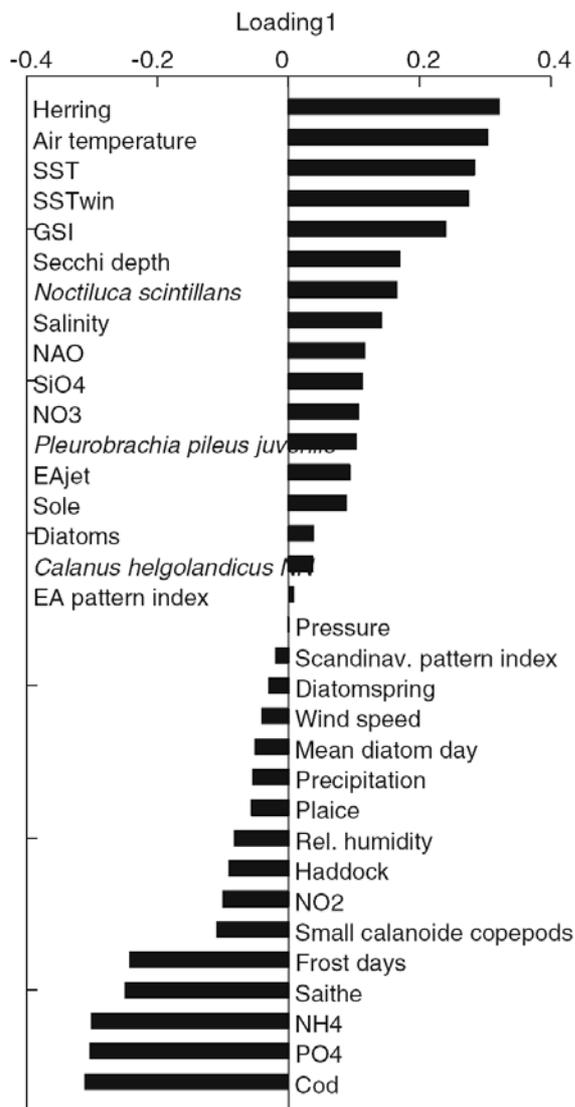


Fig. 4 Spectrum of loadings for the first principal component from a principal component analysis of the full set of variables. The corresponding variable to each loading is written next to each bar

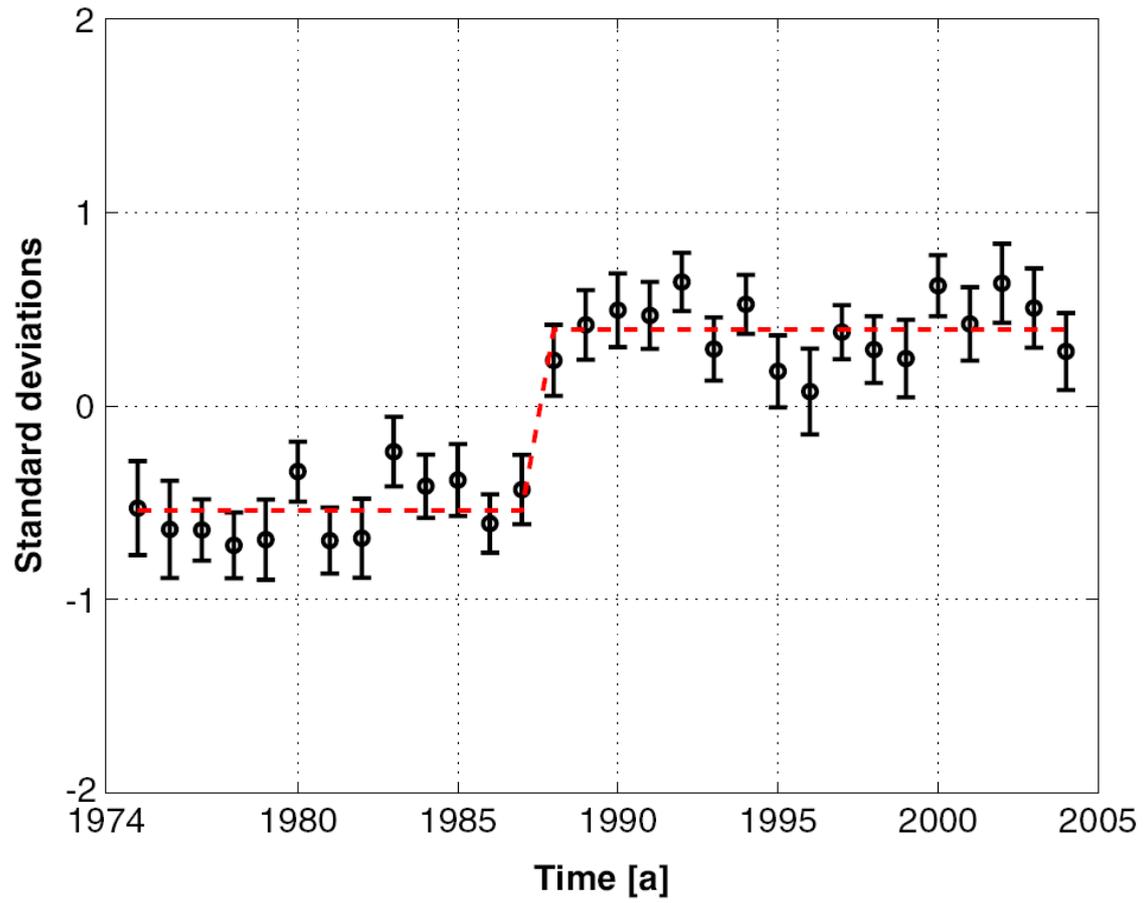


Fig. 5 Results from the regime shift analysis of the full set of variables. The step (red) passes through the mean standard deviate within each regime. The standard error of the full set of variables is presented for each year and the circles show the annual means of the standardised time series

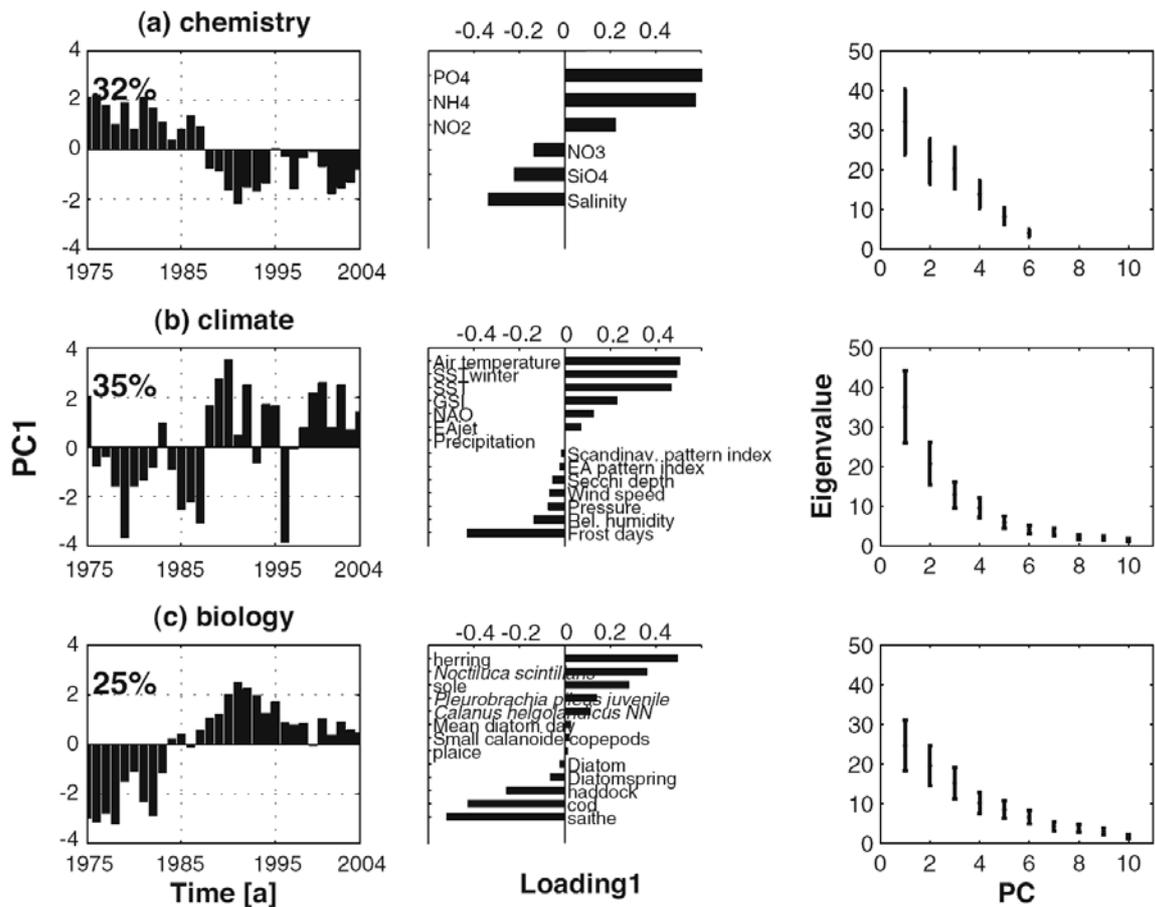


Fig. 6 The first principal component (PC1) from the principal component analysis of the separated data for chemistry (a), climate (b) and biology (c) for the period 1975 to 2004 is shown in combination with each spectrum of loading and eigenvalue scree plot

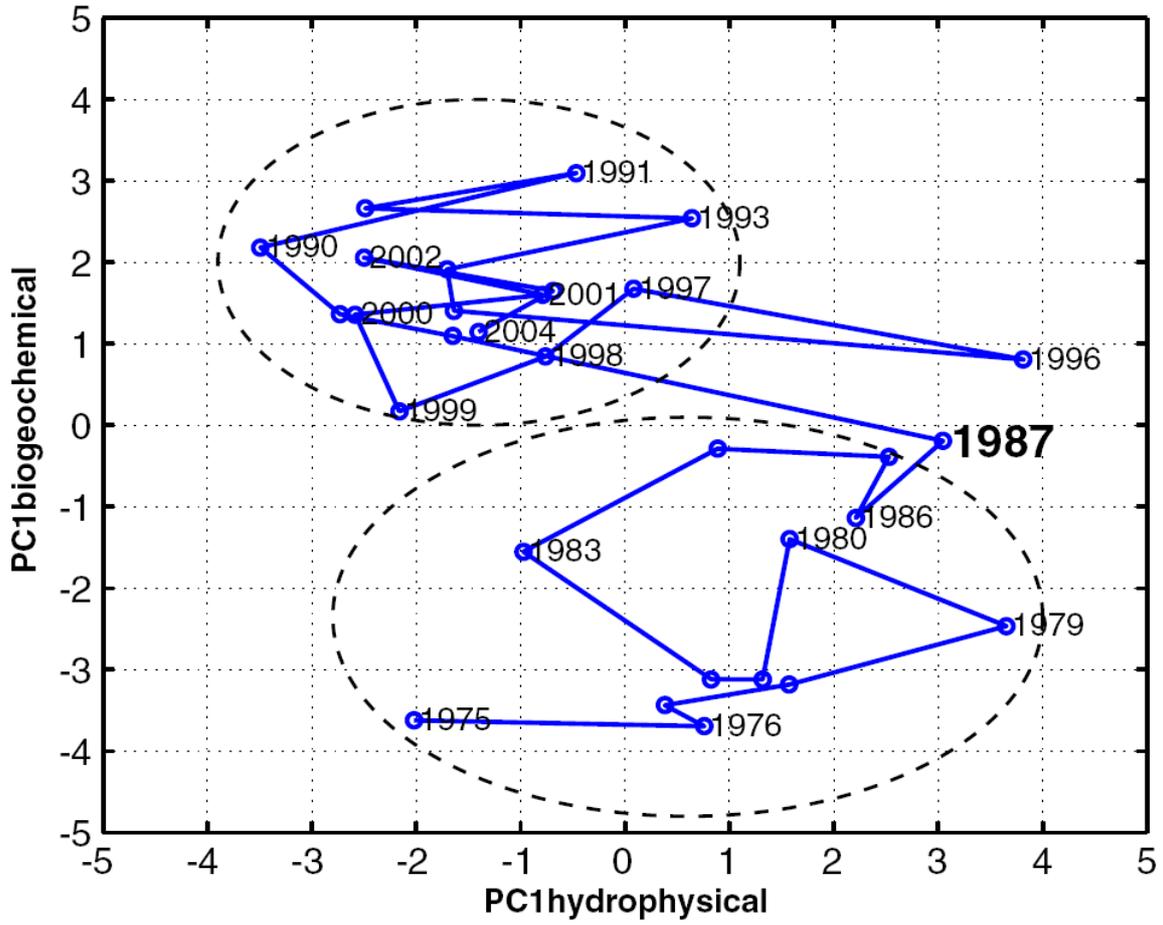


Fig. 7 Scatter plot of the first principal component of all biogeochemical variables against the first principal component of all hydrophysical data. Full circles indicate data from 1975 to 2004. The two identified regimes are surrounded with a black circle, and the tipping point (1987) around the shift is bold. Lines between the circles indicate the variability

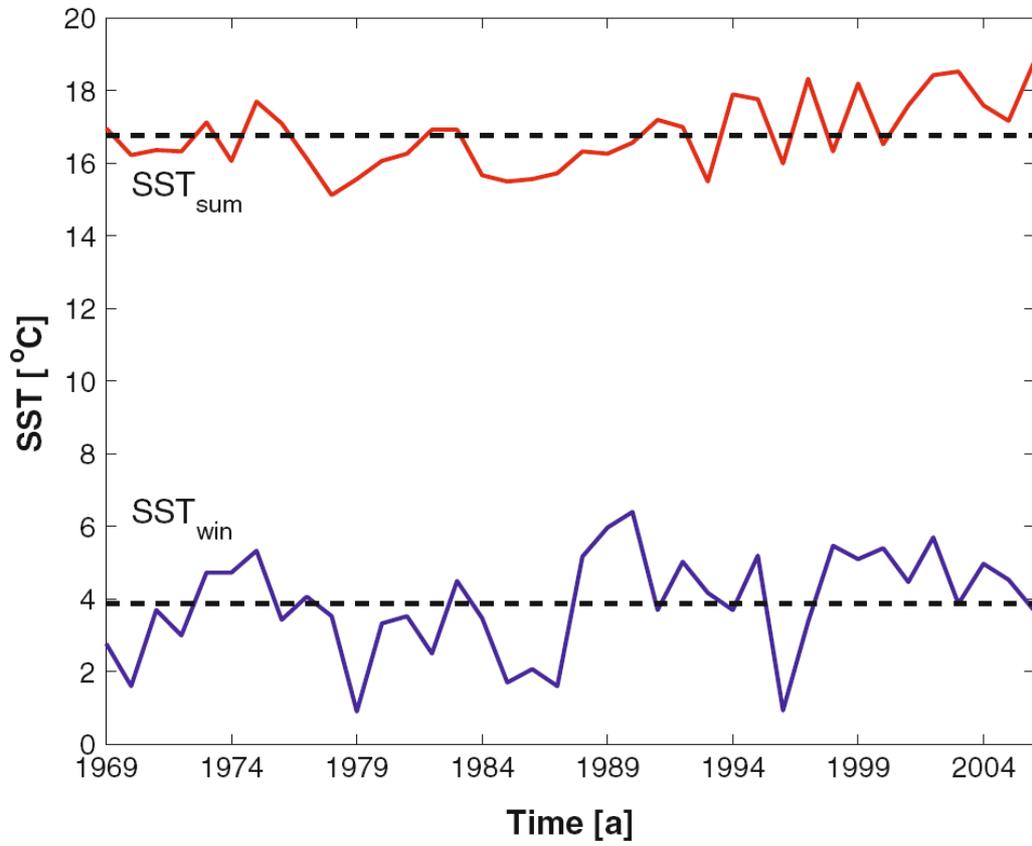


Fig. 8 Time series of seasonal winter (blue line) and summer (red line) SST for the period 1969 to 2006. The black dashed line is the mean of each seasonal SST

Appendix 1

Description of 39 physical, chemical and biological time series used in the analysis.

Table 1 Variable number, description and period

Var. no.	Description	Longitude	Latitude	Period
1	Mean winter NH ₄ at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
2	Mean winter NO ₂ at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
3	Mean winter NO ₃ at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
4	Mean winter PO ₄ at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
5	Mean winter SiO ₄ at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
6	Annual mean salinity at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
7	Annual mean diatom day of the spring bloom at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
8	Annual mean of total cell counts of diatoms at Helgoland Roads	7°54' E	54°11.3' N	1962–2002
9	Spring mean (Mar, Apr, May) of total cell counts of diatoms at Helgoland Roads	7°54' E	54°11.3' N	1962–2002
10	Annual mean <i>P. pileus</i> juvenile at Helgoland Roads	7°54' E	54°11.3' N	1975–2005
11	Annual mean <i>P. pileus</i> adult at Helgoland Roads	7°54' E	54°11.3' N	1975–2003
12	Annual mean <i>N. scintillans</i> at Helgoland Roads	7°54' E	54°11.3' N	1975–2005
13	Annual mean <i>C. helgolandicus</i> NN at Helgoland Roads	7°54' E	54°11.3' N	1975–2005
14	Annual mean <i>C. helgolandicus</i> CN at Helgoland Roads	7°54' E	54°11.3' N	1975–2003
15	Annual mean of sum of 5 small calanoid copepods at Helgoland Roads	7°54' E	54°11.3' N	1975–2005
16	Spawning Stock Biomass of cod from ICES Quadrant IV			1963–2006
17	Spawning stock biomass of herring from ICES Quadrant IV			1960–2006
18	Spawning Stock Biomass of haddock from ICES quadrant IV, IIIa			1963–2007
19	Spawning Stock Biomass sole from ICES quadrant IV			1957–2007
20	Spawning stock biomass plaice from ICES quadrant IV			1957–2007
21	Spawning stock biomass saithe from ICES quadrant IV			1967–2007
22	North Atlantic Oscillation Winter index (Dec, Jan, Feb)			1864–2006
23	Gulf Stream index			1966–2005
24	East Atlantic pattern index (Sep to Mar)			1950–2005
25	East Atlantic jet pattern index (Apr to Aug)			1950–2005
26	Scandinavia pattern index (Aug to May)			1950–2005
27	Mean annual hor. wind speed from the reg. atmos. clim. model	6°5' E–9°167' E	53°3' N–55°167' N	1948–2006
28	Annual mean air temperature at List (Sylt)	8°25' E	55°1' N	1965–200
29	Annual mean max. air temperature at List (Sylt)	8°25' E	55°1' N	1965–2006
30	Annual mean min. air temperature at List (Sylt)	8°25' E	55°1' N	1965–2006
31	Total annual sunshine duration at List (Sylt)	8°25' E	55°1' N	1965–2006
32	Total annual precipitation amount at List (Sylt)	8°25' E	55°1' N	1965–2006
33	Annual mean surface pressure at List (Sylt)	8°25' E	55°1' N	1965–2006
34	Annual mean rel. humidity at List (Sylt)	8°25' E	55°1' N	1965–2006
35	Total days with frost (min. temp. <0°C) at List (Sylt)	8°25' E	55°1' N	1965–2006
36	Mean winter Secchi disk depth at Helgoland Roads	7°54' E	54°11.3' N	1968–2006
37	Annual mean SST at Helgoland Roads	7°54' E	54°11.3' N	1962–2004
38	Annual mean SST from BSH	6°5' E–9°10' E	55°5' N–53°3' N	1969–2006
39	Mean winter (Jan, Feb, Mar) SST from BSH	6°5' E–9°10' E	55°5' N–53°3' N	1969–2006

Appendix 2

Long-term time series, sources and temporal patterns.

We analysed a total of 39 data series: 19 hydrophysical datasets comprising atmospheric, climate and hydrographic variables and 20 biogeochemical time series representing the most important levels of the ecosystem, from nutrients through phytoplankton and zooplankton to fish. We selected appropriate datasets covering 40 years, at least 30 years, up to 100 or more samples per year and no obvious anthropogenic cause for sudden changes in a dataset. Detailed information for each time series is given below in the following format: the variable number as in Table 1 in Appendix 1, detailed description, followed by the series name and source of origin. At the end of this appendix, we show the pattern of each time series for the time period for analysis standardised to zero mean and unit standard deviation. At the end of this Appendix, we show the pattern of each time series for the time period for analysis standardised to zero mean and unit standard deviation (see Figs. A2.1–A2.9).

Biogeochemical indices

Prior to data analysis, all biological time series were logtransformed to approximate linear distribution.

Chemistry

At the Biological Institute of Helgoland, the only offshore island of the North Sea, an observing monitoring program was initiated in 1962 taking samples of nutrients and phytoplankton at Helgoland Roads (HR; 54°11.3 N, 7°54 E). Phytoplankton, nutrients and Secchi disk depth have been measured every working day since 1975. These HR long-term time series are one of the most extensive datasets currently available (see also Wiltshire 2004). The single spot high frequency, length and satisfactory data quality of the HR time series allow the detection of weak long-term overall trends and is an invaluable source of quantitative information on ecosystem function (Wirtz and Wiltshire 2005).

The nutrient data are quality-checked (see Raabe and Wiltshire 2008) for possible gaps, leaps and discontinuities with a variety of statistical and graphical plot procedures. In addition, a direct correlation with data sampled in a “reference area” nearby Helgoland Stations and obtained by different sources was performed in order to identify general divergences of the two independent datasets (Raabe and Wiltshire 2008). No obvious anomalies suggesting strong inhomogeneity were reported in the data.

1. Long-term annual winter mean of NH₄ concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

2. Long-term annual winter mean of NO₂ concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

3. Long-term annual winter mean of NO₃ concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

4. Long-term annual winter mean of PO₄ concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

5. Long-term annual winter mean of SiO₄ concentration as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

6. Long-term annual mean of salinity as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005)

Phytoplankton

7. Long-term annual mean diatom day (MDD) of the algal spring bloom as calculated by Wiltshire and Manly (2004) from algal measurements every work day at Helgoland Roads. MDD is defined as $MDD = \sum f_i d_i / \sum f_i$, where f_i is the diatom count on day d_i of the quarter of the year, and the sum is over the available samples in the quarter (see Wiltshire and Manly 2004 for more explanation).

Source: Wiltshire and Manly (2004)

8. Long-term annual mean of total cell counts of diatoms as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005) and Wiltshire and Dürselen (2004)

9. Long-term spring mean (Mar, Apr and May) of total cell counts of diatoms as measured every work day at Helgoland Roads.

Source: Wirtz and Wiltshire (2005) and Wiltshire and Dürselen (2004)

Zooplankton

The HR zooplankton time series is a high-frequency (every Monday, Wednesday and Friday), fixed position monitoring and research programme. The distance to the coastline permits these data as indicators of the surrounding German Bight plankton populations (Greve et al. 2004). Samples were taken with a 150- μ m mesh Hydrobios plankton handnet (NN) and 500- μ m mesh calcofinet (CN) for zooplankton at 54°11.18 N, 7°54 E.

10. Long-term annual mean of *Pleurobrachia pileus* juvenile in individuals per cubic metre as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

11. Long-term annual mean of *Pleurobrachia pileus* adult in individuals per cubic metre as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

12. Long-term annual mean of *Noctiluca scintillans* in individuals per cubic metre as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

13. Long-term annual mean of *Calanus helgolandicus* NN in individuals per cubic metre as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

14. Long-term annual mean of *Calanus helgolandicus* CN in individuals per cubic metre as measured three times a week at Helgoland Roads.

Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

Five small calanoid copepods (*Paracalanus parvus*, *Pseudocalanus elongatus*, *Centropages* spp., *Acartia* spp. and *Temora longicornis*) are representative for the dominant small calanoid populations of the German Bight. The sum of the abundance of the population of calanoid copepods renders a basic pattern of changes in the pelagic ecosystem (Greve et al. 2004).

15. Long-term annual mean of the sum of the abundance of small calanoid copepods: *Paracalanus parvus*, *Pseudocalanus elongatus*, *Centropages* spp., *Acartia* spp. and *Temora longicornis* in individuals per cubic metre as measured three times a week at Helgoland Roads.
Source: Wulf Greve, Research Institute Senckenberg, Germany (unpublished)

Fishes

ICES fish data are generally used to estimate the size of commercial fish populations. This work is coordinated internationally, and independent review groups check the results. The North Sea is divided into a grid of rectangles which will be sampled a number of times with the same trawling gear. Mathematical models are then used to transform these records into population estimates. For more information, see www.ices.dk.

Spawning stock biomass (SSB) in 1,000 t year⁻¹

16. SSB of North Sea cod from ICES quadrant IV
17. SSB of North Sea herring from ICES quadrant IV
18. SSB of North Sea haddock from ICES quadrants IV and IIIa
19. SSB of North Sea sole from ICES quadrant IV
20. SSB of North Sea plaice from ICES quadrant IV
21. SSB of North Sea saithe from ICES quadrant IV.

Source: <http://www.ices.dk/committe/acfm/comwork/report/asp/advice.asp>

Hydrophysical indices

Atmospheric indices

The North Atlantic Oscillation (NAO) is one of the major modes of variability of the Northern Hemisphere atmosphere. Ottersen et al. (2001) concluded that the NAO has a strong influence on ecological dynamics and that it causes diverse responses in ecological processes, ranging from the timing of reproduction to spatial distribution of biological communities. The NAO index is defined on the difference of normalised atmospheric sea level pressure (SLP) between Ponta Delgada, Azores and Stykkisholmur/Reykjavik. The climate condition in the winter season has the greatest influence on biological processes. The SLP anomalies at each station were normalised by division of each seasonal mean pressure by the long-term mean standard deviation. Normalisation is used to avoid the series being dominated by the greater variability of the northern station. High values of the index indicate stronger-than-average westerlies over the middle latitudes because the subtropical high pressure centre is stronger than normal and the Iceland low is deeper than normal. In the North Sea, the dominant atmospheric circulation is

anticyclonic. The intensity of the NAO may also be correlated with the mean wave height which contributes to the mixing of water masses.

22. North Atlantic Oscillation Winter Index (Dec., Jan. and Feb.)

Source: <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>

The GSI is an indicator of the North–South shifts in the latitude of the north wall of the Gulf Stream between 79° W and 55° W (Taylor and Stephens 1980; Taylor 1995, 1996). The GSI contributes to the heat and salinity transport into the North Sea.

23. Gulf Stream index

Source: <http://web.pml.ac.uk/gulfstream/data.htm>.

The East Atlantic pattern index appears as a low frequency variability over the North Atlantic from September to April. It is the second of three primary modes.

24. East Atlantic pattern index (Sep. to Mar.)

Source: <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/>

The East Atlantic jet pattern index appears from April to August as the third primary mode of low-frequency variability over the North Atlantic.

25. East Atlantic jet pattern index (Apr. to Aug.)

Source: <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/>

The Scandinavia pattern index appears from August to May as a primary mode of low-frequency variability over Scandinavia and western Russia.

26. Scandinavia pattern index (Aug. to May)

Source: <http://www.cpc.noaa.gov/data/teledoc/scand.shtml>

Climatic indices

The German Weather Service (DWD) monitors stations all over Germany. The climatic variables are from the coastal station List on the island Sylt in the German Bight. There were no site moves of the station during the selected time period. Except for wind speed, we took the reconstructed horizontal wind speed data from the regional atmospheric climate model (SN-REMO) with spectral nudging with a horizontal resolution of 0.5 because the output is dynamically consistent. For more information, see <http://www.coastdat.de/dhome.html> . Wind measurements depend to a great extent on the details of the surroundings (e.g. exposition and obstacles), which influence the data homogeneity.

27. Mean annual horizontal wind speed

Source: <http://www.coastdat.de> , Feser et al. (2001)

28. Annual mean air temperature

29. Annual mean maximum air temperature

30. Annual mean minimum air temperature

31. Total annual sunshine duration
 32. Total annual precipitation amount
 33. Annual mean surface pressure
 34. Annual mean relative humidity
 35. Total days with frost from November to March
- Source: DWD Offenbach, <http://www.dwd.de>

Hydrographic indices

Secchi disk depth readings are affected by the sensitivity of the human eye which, in turn, may affect the visual contrast between the disk and the surrounding water in water bodies of varying spectral light transmission properties and between observers at the same water body. As argued by Tilzer (1998), these variations cannot be eliminated; however, comparative readings by inexperienced students in Lake Constance have shown a relatively narrow margin of subjective error (standard deviation of mean value $\pm 8\%$).

36. Long-term annual winter mean Secci disk depth as measured every work day at Helgoland Roads.

Source: Karen H. Wiltshire, Biological Institute of Helgoland, Germany (unpublished)

37. Annual average sea surface temperature (in °C) at 54°11.3 N, 7°54 E (Helgoland Roads) measured every work day.

Source: Wirtz and Wiltshire (2005)

38. Annual average sea surface temperature (in °C) for the German Bight (6°5 E to 9°10 E and 55°5 N to 53°3 N) from the Bundesamt für Seeschifffahrt und Hydrographie (BSH).

Source: Peter Loewe, BSH, Hamburg, Germany

39. Mean winter (Jan., Feb. and Mar.) sea surface temperature (in °C) for the German Bight (6°5 E to 9°10 E and 55°5 N to 53°3 N) from the Bundesamt für Seeschifffahrt und Hydrographie (BSH)

Source: Peter Loewe, BSH, Hamburg, Germany

The SST variability at Helgoland Roads was very similar to the SST pattern for the German Bight provided by the BSH. The SST from BSH comprised the largest German Bight area though and we omitted the SST from Helgoland Roads. Since 1968, the BSH provides weekly quasi-synoptical charts of SST. The data were calculated from SST grids of 20 m² with the aim of obtaining an accurate insight into the spatio-temporal evolution (Loewe and Becker 2003). Here, we use monthly averages of these data (Peter Loewe, BSH, personal communication) to obtain annual averages. Some biological processes are linked with winter SSTs. For that, we included the seasonal average as well.

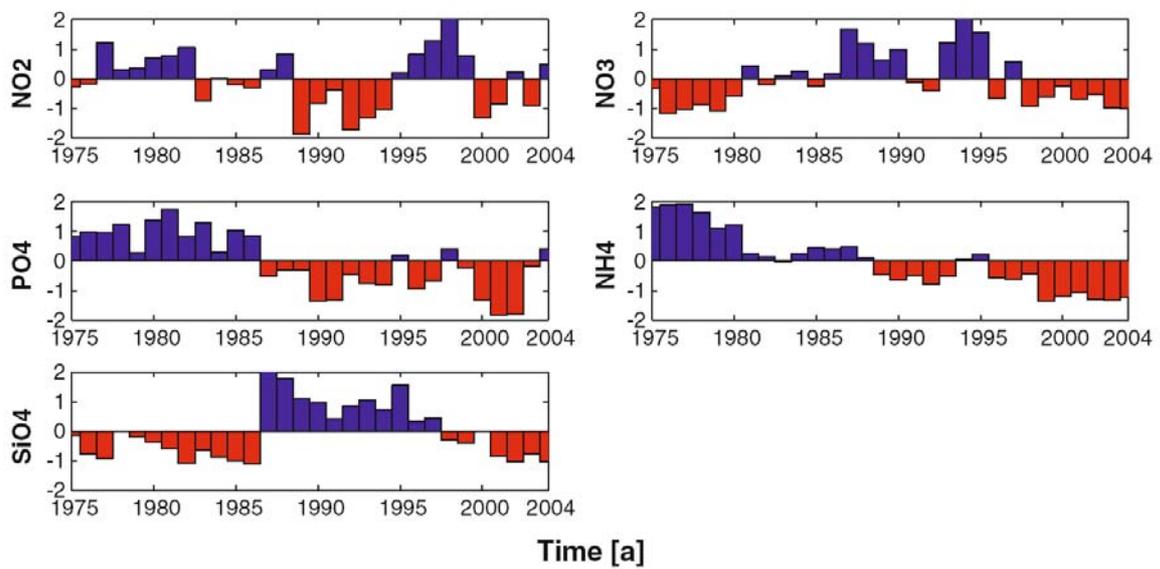


Fig. A2.1 Time series of annual mean of NO₂, NO₃, PO₄, NH₄ and SiO₄ at Helgoland Roads standardised to zero mean+1 SD for the period 1975 to 2004

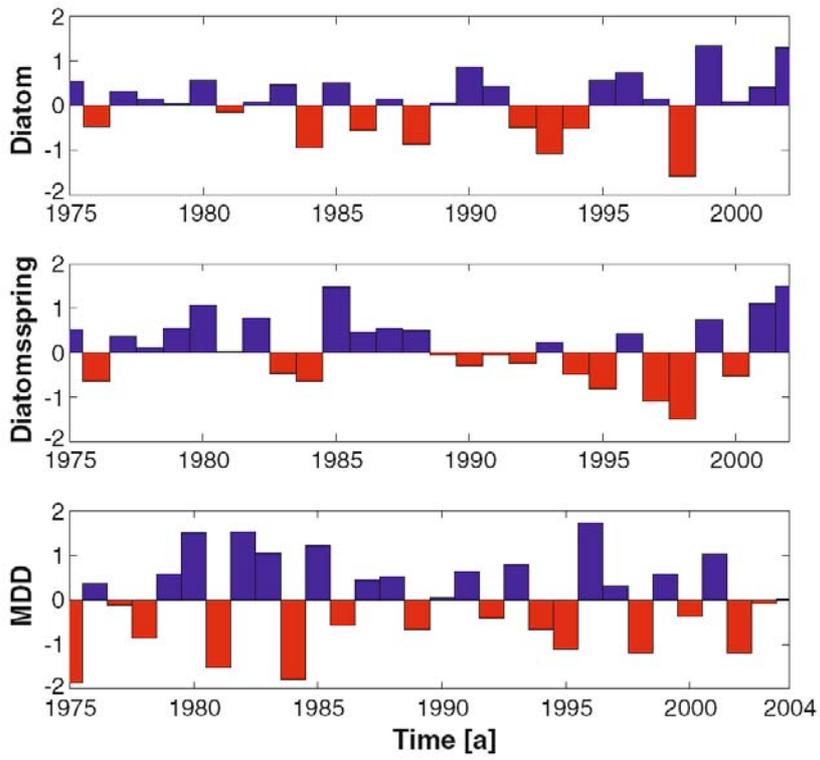


Fig. A2.2 Time series of annual mean of diatoms, mean of spring diatoms and MDD of the diatom spring bloom at Helgoland Roads standardised to zero mean+1 SD for the period 1975 to 2004

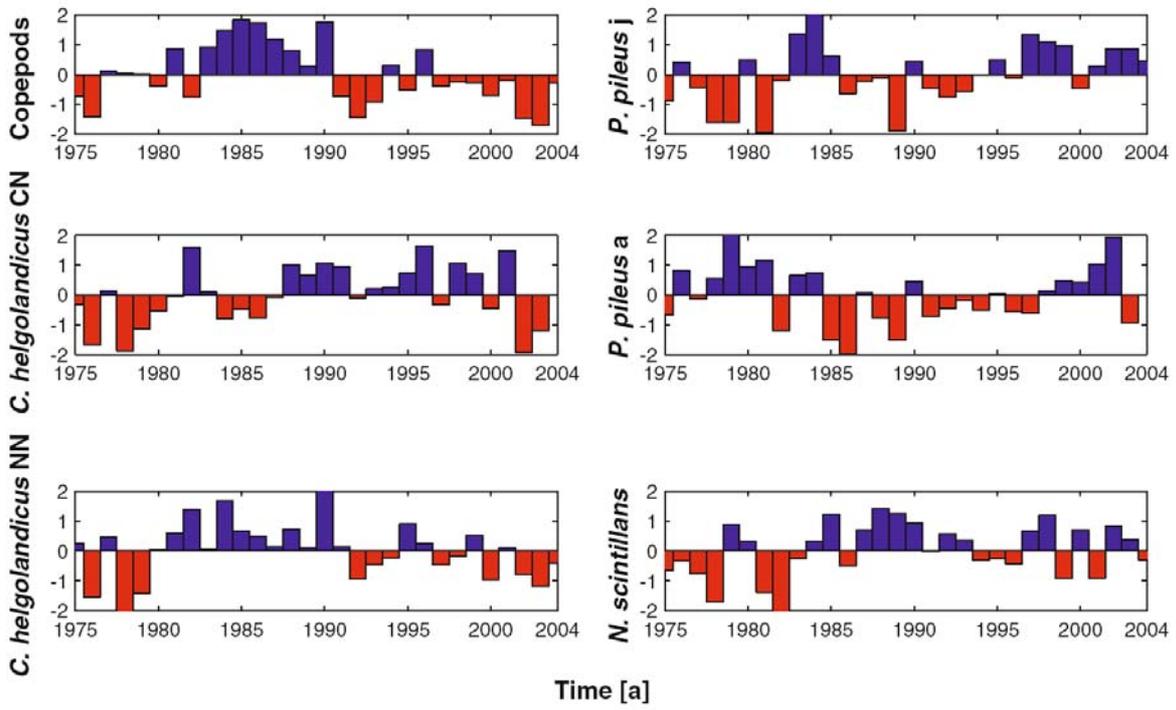


Fig. A2.3 Time-series of annual mean of the sum of the abundance of five small calanoid copepods and of *P. pileus* juvenile, *C. helgolandicus* CN, *P. pileus* adult, *C. helgolandicus* NN and *N. scintillans* at Helgoland Roads with zero mean+1 SD

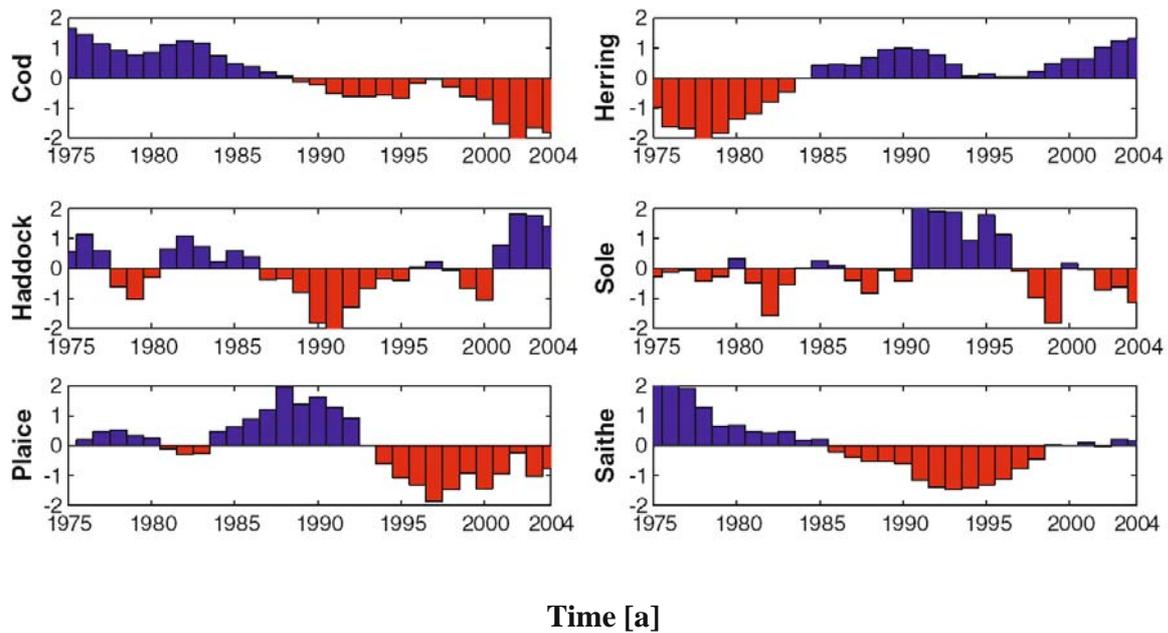


Fig. A2.4 Time series of SSB of cod, herring, haddock, sole, plaice and saithe in the North Sea standardised to zero mean+ 1 SD for the period 1975 to 2004

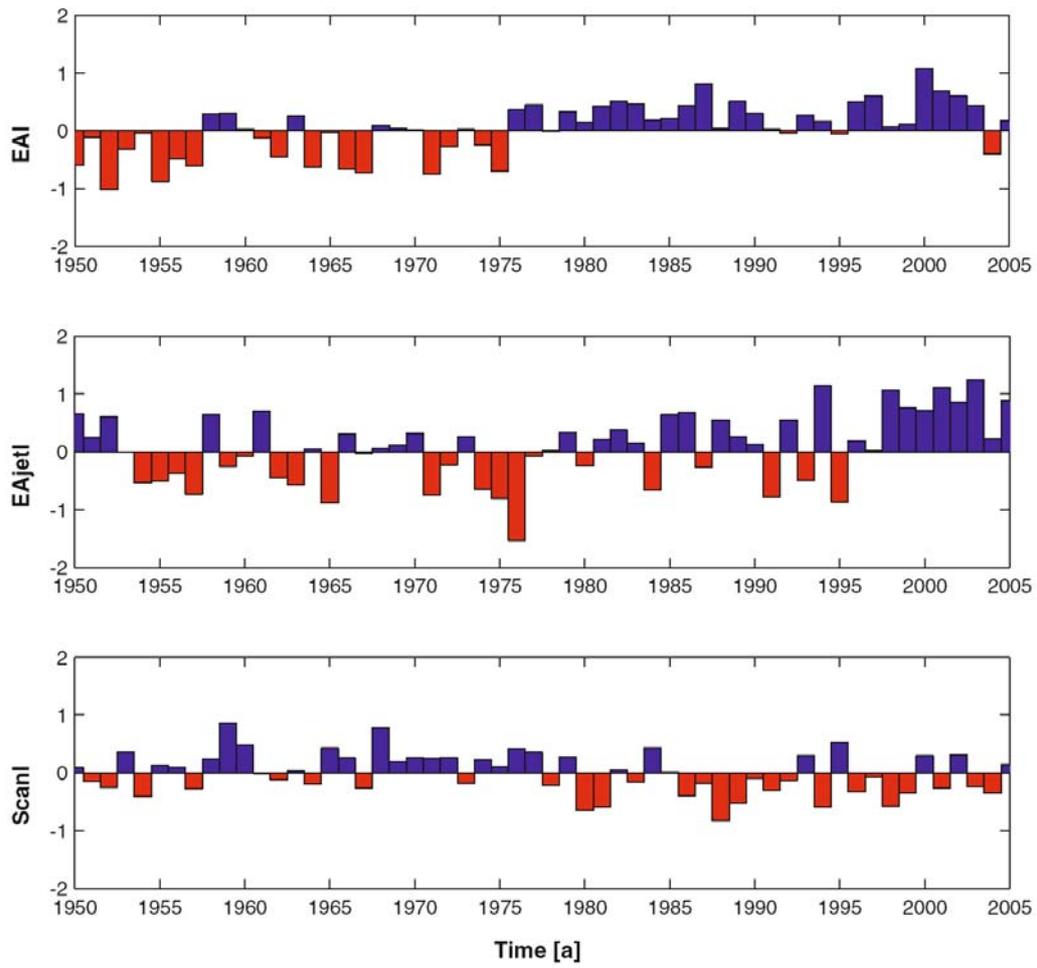


Fig. A2.5 Time series of East Atlantic pattern index (EAI), East Atlantic jet pattern index (EAjet) and Scandinavian pattern index (ScanI) with zero mean+1 SD for the period 1950 to 2005

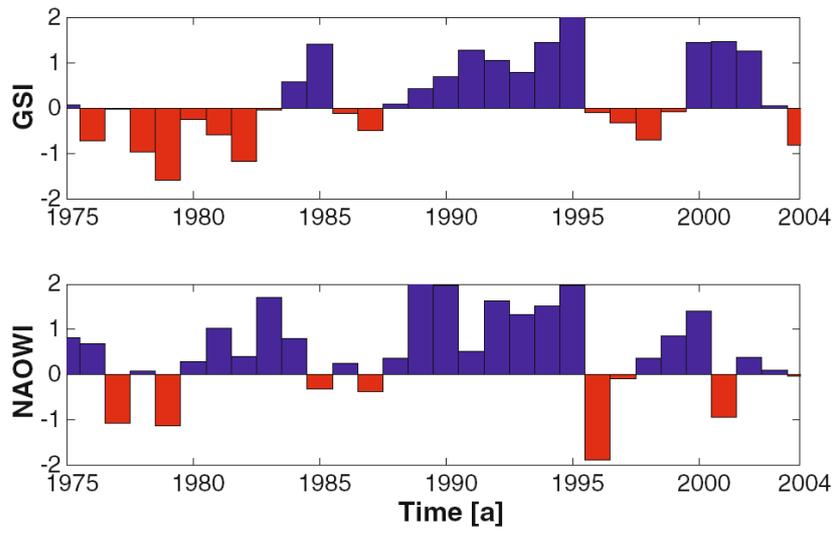


Fig. A2.6 Time series of the Gulf Stream index (GSI) and North Atlantic Oscillation Index (NAOWI) with zero mean+1 SD for 1975 to 2004

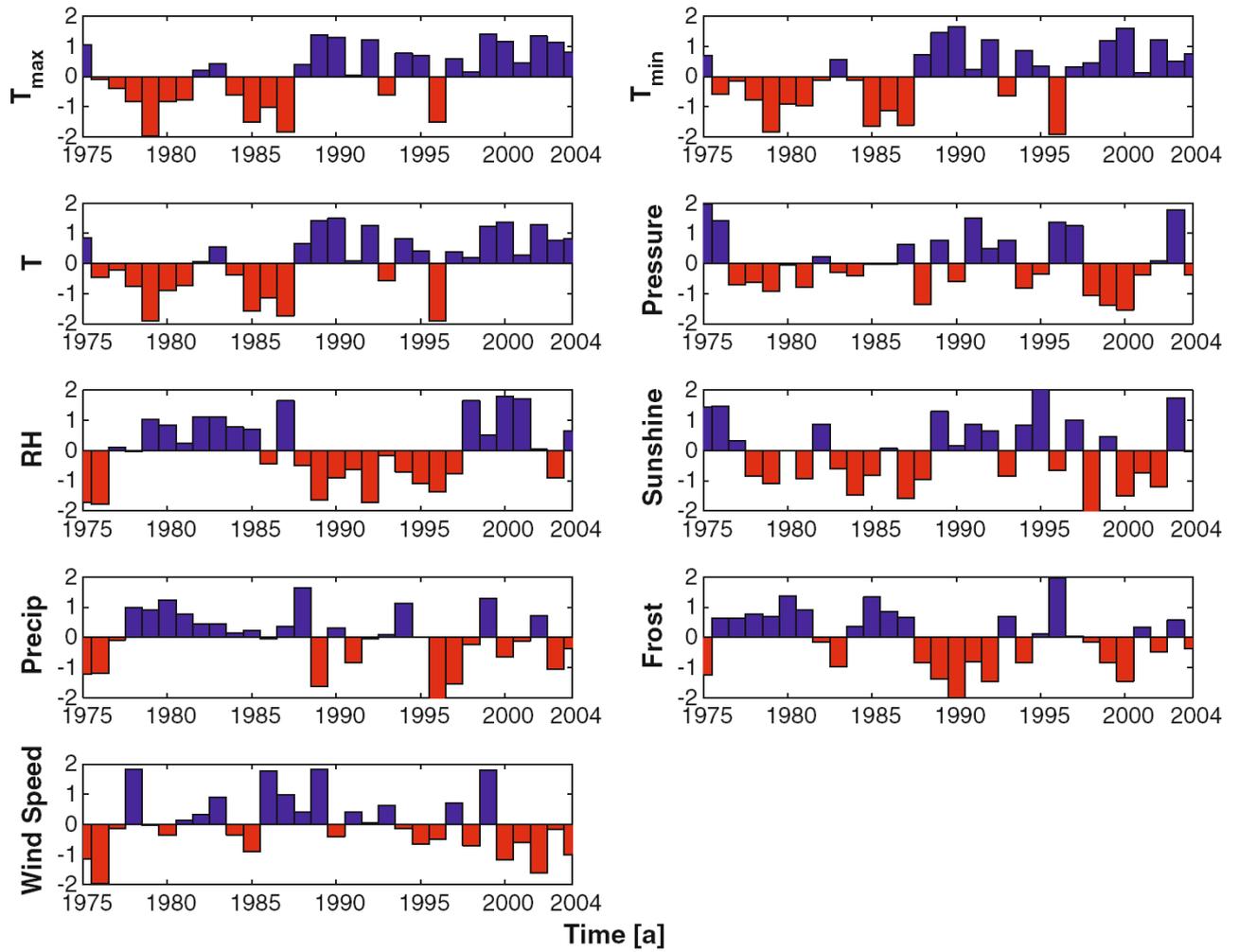


Fig. A2.7 Time series of the annual mean of nine atmospheric variables: maximum air temperature, minimum air temperature, air temperature, pressure, relative humidity, total sunshine duration, precipitation amount, frost days at List/Sylt and wind speed for the German Bight with zero mean+1 SD from 1975 to 2004

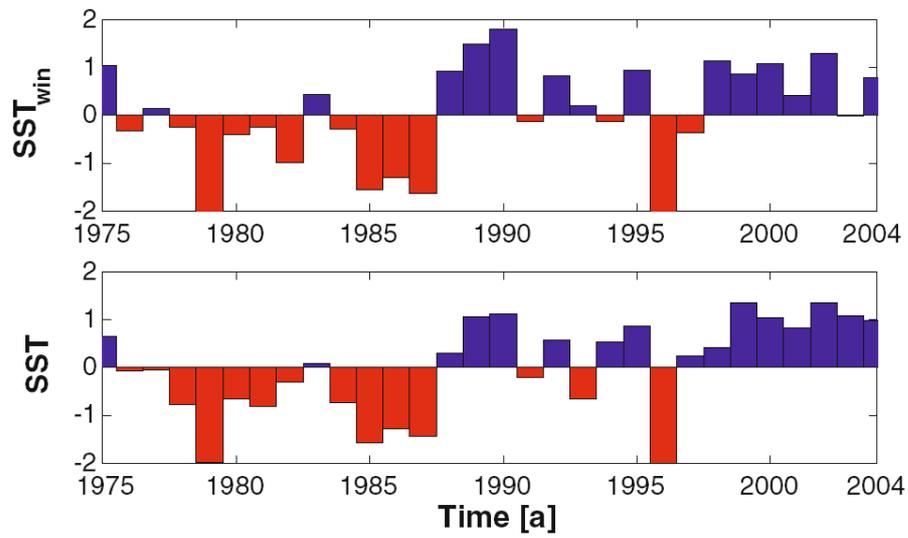


Fig. A2.8 Time series of mean winter and annual sea-surface temperature for the German Bight with zero mean+1 SD for 1975 to 2004

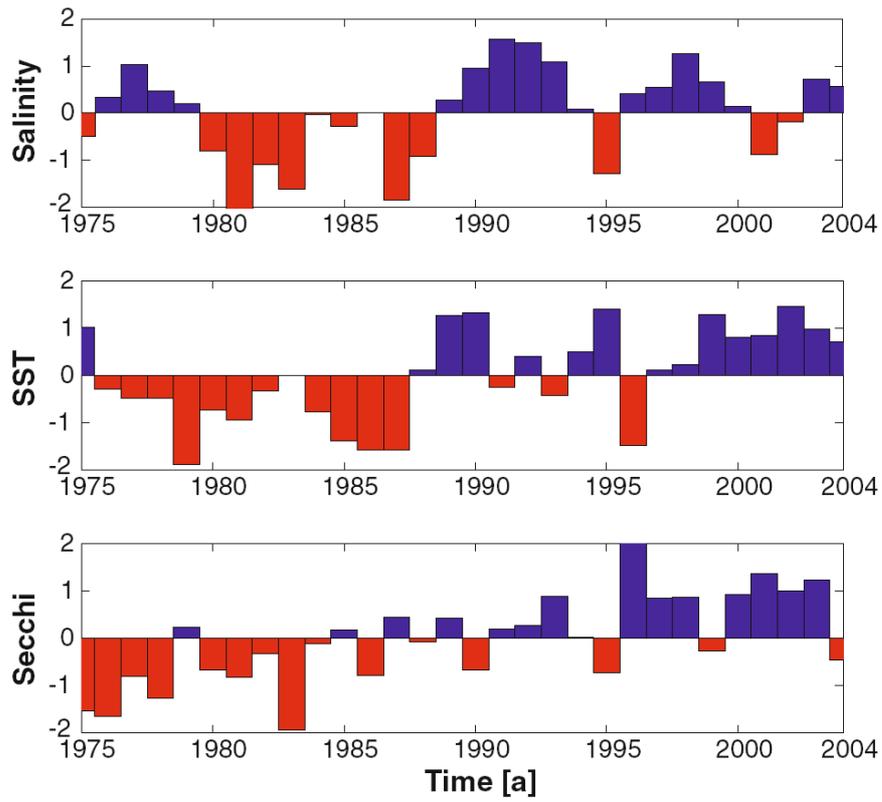


Fig. A2.9 Time series of annual mean salinity, sea-surface temperature and Secchi disk depth at Helgoland Roads with zero mean+1 SD for 1975 to 2004

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