

# Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003

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**ABSTRACT:** Global warming is now unequivocal, and studies suggest it has started to influence natural systems, including the oceans. Here, we quantify plankton changes in the North Sea for the period 1958 to 2007 using an approach we call Multi-Scale Multivariate Split Moving Window (MMS-SMW) analysis that we apply to 5 groups: (1) diatoms, (2) dinoflagellates, (3) copepods, (4) other holozooplankton and (5) meroplankton. Three temporally persistent shifts were identified in the 1960s, the 1980s and during the period 1996 to 2003. The present study therefore reveals for the first time an abrupt ecosystem shift between 1996 and 2003 in the North Sea, which had the same magnitude in terms of species response as the well-documented shift detected in the 1980s. All ecosystem shifts coincided with a significant change in hydro-climatic conditions and had consequences for the structure and the functioning of the ecosystems. We showed that the 3 shifts only impacted 40% of the plankton species or taxa considered in the analysis and that the timing of the shift varied according to the planktonic group and even among species within a group.

**KEY WORDS:** Abrupt ecosystem shift · Plankton · Climate · Multiscale Split Moving Window Boundary analysis

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## INTRODUCTION

Marine ecosystems fluctuate in space and time. These fluctuations originate from the inherent properties of the ecosystems and external factors such as climate and, more recently, human activities (Cury et al. 2003, Brander 2007, Beaugrand 2009). The influence of climate on the structure, biodiversity and functioning of marine ecosystems has been documented (Beaugrand et al. 2010). Climatic variations have also been associated with large-scale regime shifts (Hare & Mantua 2000, Reid et al. 2001, Beaugrand et al. 2002). Regime shifts have been defined as a rapid and substantial change in the state of an ecosystem, the state lasting longer than the transitional period (deYoung et al. 2004). Reid et al. (2001) were

the first to propose that an ecosystem shift may have happened in the North Sea ca. 1988. They based their hypothesis on many changes that were observed in the biological composition of North Sea marine ecosystems at the end of the 1980s (e.g. Lindley et al. 1990, 1993, Greve 1994). Beaugrand, Weijerman and colleagues subsequently documented and tested statistically the magnitude of this abrupt ecosystem shift (Beaugrand 2004b, Beaugrand & Ibanez 2004, Weijerman et al. 2005, Beaugrand et al. 2008). While the first research team mainly focussed on some key plankton species, the second used a large range of indicators from plankton to higher trophic levels along with a broad range of abiotic parameters. The latter authors used a global (i.e. based on a multitude of parameters analysed globally) statistical approach based on tech-

niques such as principal component analysis (PCA) and cluster analysis.

The term regime shift implicitly assumes that stable states (or regimes) exist (Beaugrand 2004b). This can be the case in lakes where a system dominated by submerged plants can alternate with a system dominated by phytoplankton, each stable state being characterised by specific nutrient dynamics and level of turbidity (Scheffer & van Nes 2004). Different stable states may also be clearly perceived in some marine ecosystems, e.g. in tropical benthic ecosystems where a system can switch from a coral-dominated to an algal-dominated ecosystem when both nutrient loading and fishing pressures increase (Nyström et al. 2000). While for lakes and some benthic ecosystems where engineer or keystone species have a critical influence on the system, the concept of regime shifts is relatively well defined, this is apparently more complex for pelagic ecosystems because they are not structured and controlled in the same way. Some systems can change substantially, but it remains difficult to rapidly detect their switches because their stable states are less apparent (Hare & Mantua 2000, Reid et al. 2001, Beaugrand et al. 2008). This led Beaugrand et al. (2008) to characterise a shift by its multiscale and multivariate variance signature, assuming that ecosystems vary all the time at all spatial and temporal scales but that there are periods when changes accelerate. For this phenomenon they proposed the term 'abrupt ecosystem shift' (AES). In practice, there are many different kinds of AESs. AESs can be related to episodic events, also named ocean climate anomalies (Edwards et al. 2002). Such an event took place in the North Sea during the period 1978 to 1982 and was characterised by the occurrence of cold-water plankton (Edwards et al. 2002). Profound ecosystem changes can also have a longer temporal persistence. This was the case in the North Sea when the system switched in the 1980s from a cold dynamic regime (1962 to 1982) to a warmer dynamic regime (1990 onward) (Reid et al. 2001, Beaugrand 2004b, Weijerman et al. 2005). During an AES, the variability increases; however, the adjective 'abrupt' does not mean that the transition occurs in a single year but instead that rates of biological changes accelerate. Other types of ecosystem shifts include sardine-anchovy cycles in upwelling systems where changes in hydro-climatic forcing and fishing are thought to be the main drivers (Chavez et al. 2003, Alheit 2009). However, it can be more difficult to identify these changes as an AES because the critical transition can take more time. In the present study, we opera-

tionally define an AES as a relatively rapid change in the state of an ecosystem, the duration of the state being variable so as to include in the classification all the phenomena listed above.

When a large number of biological variables are investigated, methods such as PCA or cluster analyses have been generally applied to detect AESs (Mantua 2004, Weijerman et al. 2005). However, such methods mask the fact that many species do not change at the time of an AES. Many statistical approaches for identifying an AES also require the use of an arbitrary time window, producing different results (Webster 1973, Legendre & Legendre 1998). In the present study, we used a technique for identifying an AES that takes into account the community responses of the entire plankton. This approach was applied to evaluate the long-term changes (1958 to 2007) in the plankton. Plankton was divided into 5 taxonomic components: (1) diatoms, (2) dinoflagellates, (3) copepods, (4) other holozooplankton and (5) meroplankton. We modified Webster's sliding moving window boundary analysis (Webster 1973) to quantify the abrupt shifts for each taxonomic group at the species level using a multiscale approach. The technique identified 2 already documented shifts and revealed a new one that took place between 1996 and 2003, paralleling a pronounced increase in global temperature.

## MATERIALS AND METHODS

### Studied area

We investigated the long-term changes in plankton composition and abundance in the North Sea (3° W to 10° E and 51° N to 60° N).

### Biological data

Biological data used in the present study were collected by the Continuous Plankton Recorder (CPR) survey. This large-scale plankton-monitoring programme has sampled the upper layer of the water column (~7 m) on a monthly basis since 1946 (Warner & Hays 1994, Reid et al. 2003). Details on the methods and contents of this dataset are provided by Reid et al. (2003) and Batten et al. (2003).

Changes in the abundance of all species or taxonomic groups included in the CPR survey were investigated. An annual mean was calculated for all species or taxa using a procedure similar to the Copepod Indicator Monitoring Toolbox System des-

cribed by Beaugrand (2004a). This statistical method allows the construction of a time series for a given plankton species in the region covered by the CPR survey. The algorithm minimises the effect of the spatial and temporal heterogeneity of the sampling protocol by randomly selecting a constant number of samples, fixed here to 5 samples (Beaugrand 2004a). All species time series were first assessed for each month of the period from 1958 to 2007. We then calculated an annual mean based on 12 mo, each month being based on the same number of CPR samples. We chose to base the annual averages on all months because species have distinct seasonal maxima. Then, species or taxa with an annual relative abundance  $>0.001$  and a presence  $>30\%$  for all years from 1958 to 2007 were selected using the procedure applied by Ibanez & Dauvin (1998). The choice of these thresholds was exclusively conditioned by the statistical techniques, which should not be applied on data matrices containing a proportion of zeroes that is too large. This procedure allowed the selection of 73 species or taxonomic groups (33 diatom species, 11 dinoflagellate species, 14 copepod species and 15 other zooplankton taxa including fish eggs and larvae). Abundance data in the matrix (50 years  $\times$  73 species or taxa) were transformed using the function  $\log_{10}(x + 1)$ .

### Physical data

Annual sea surface temperature (SST) data were used because temperature has a large influence on many biological and ecological systems (Brown et al. 2004). Annual SST data come from the Comprehensive Ocean-Atmosphere Data Set (COADS,  $1^\circ$  enhanced data) (Woodruff et al. 1987). Three large-scale hydro-climatic indices were used in the present study: (1) the winter North Atlantic Oscillation (NAO) index is the result of a PCA performed on sea level pressure over the North Atlantic sector from December to March (Hurrell et al. 2001); (2) the Northern Hemisphere Temperature (NHT) anomalies from 1958 to 2007 were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, Exeter, UK; (3) the Atlantic Multidecadal Oscillation (AMO) is a large-scale oceanic phenomenon, that is a source of natural variability in the range of  $0.4^\circ\text{C}$  in many oceanic regions (Enfield et al. 2001). We used the index constructed from Extended Reconstruction SST (ERSST) data and averaged in the area of  $25$  to  $60^\circ\text{N}$  and  $7$  to  $75^\circ\text{W}$ , minus regression on global mean temperature (NCDC, <http://climexp.knmi.nl/>).

### Identification of long-term changes in plankton composition and abundance

The identification of long-term changes in plankton composition and abundance was undertaken by means of a standardised PCA. Five PCAs were performed on (1) diatoms (matrix 50 years  $\times$  33 species or taxa), (2) dinoflagellates (matrix 50 years  $\times$  11 species or taxa), (3) copepods (matrix 50 years  $\times$  14 species or taxa), (4) other holozooplankton (matrix 50 years  $\times$  9 species or taxa) and (5) meroplankton (matrix 50 years  $\times$  5 species or taxa). In the 5 analyses, the 4 physical indices (i.e. annual SST, NAO, NHT and AMO) were added as supplementary variables (Beaugrand & Ibanez 2004). We calculated the linear correlation (Pearson correlation coefficient) between all physical indices and the first 2 principal components. Thus, the physical indices had no weight in the calculation of the principal components. The eigenvalues of each principal component indicated the percentage of species that followed the pattern exhibited by the principal component. The eigenvalues are indicated in the figure legends.

### Identification and quantification of abrupt ecosystem shifts

Abrupt changes (also called temporal discontinuities) were identified using a modified version of Webster's numerical procedure called Split Moving-Window boundary (SMW) analysis (Webster 1973). This method was applied by Beaugrand (2003) and Beaugrand & Ibanez (2004) to detect temporal discontinuities. SMW, proposed originally by Webster (1973), is usually performed in 4 steps. (1) A time period of even-numbered size is introduced at the beginning of the time series. (2) This period is then divided into 2 windows. (3) A comparison of means is performed between the 2 windows. While the Multiple-Response Permutation Procedure (MRPP) (Mielke et al. 1981) can be applied (Beaugrand 2003, Beaugrand & Ibanez 2004), we used here the Kruskal-Wallis test (Sokal & Rohlf 1995) to compare the 2 periods, which is equivalent to the MRPP in the univariate case. (4) The window is then moved from year to year, repeating Steps 2 and 3 until the procedure reaches the end of the time series. However, this method has been criticised because results may vary according to the selection of the windows (Cornelius & Reynolds 1991). To take this important criticism into consideration, we applied the analysis for a range of windows. We also used this technique at the species

level and displayed the results in a contour diagram that represents the time windows versus years for all species combined together and at the statistical thresholds of 5% (see Figs. 5C–9C), 1% and 0.5% (see Fig. 10). The results were expressed as the number or the percentage of species that exhibited a significant discontinuity. In this way, it is possible to examine how the probability of an AES changes as a function of the length of the time window (here expressed as the number of years). When a shift occurs at a small scale (i.e. for small time windows and therefore few years), it indicates an episodic event or an anomaly (Edwards et al. 2002). When the shift occurs at large time windows, it indicates that an abrupt shift is persistent in time. We name this technique Multi-Scale Multivariate Split Moving-Window boundary (MMS-SMW) analysis. We applied MMS-SMW on plankton annual time series. Applied at a monthly scale, the analysis would have detected a shift between winter and summer each year.

To detect AESs among the 5 plankton groups, we ran the MMS-SMW analysis for each species and retained only species that exhibited a significant change using a probability threshold of 5% for a given year and time window (see Figs. 5–9). We represented the results as the number of species showing a significant shift as a function of the scale (i.e. time windows) and years. We also applied the technique using different levels of probability ( $p = 0.05$ ;  $p = 0.01$ ;  $p = 0.005$ ) to examine the potential influence of temporal autocorrelation on the results.

### Theoretical examples to understand how to interpret results from MMS-SMW

We generated a number of random and perturbed time series with a varying degree of temporal autocorrelation to explain how to interpret MMS-SMW in a large variety of situations. We started with 4 cases for which time series (100 time units) were not temporally autocorrelated.

**Case 1: random fluctuations.** Fifty time series with random temporal fluctuations ranging from 0 to 1 were simulated (see Fig. 1A). No clear pattern should emerge.

**Case 2: abrupt ecosystem shift.** Fifty time series with random temporal fluctuations of magnitude ranging from 0 to 2.5 (arbitrary unit) and a discontinuity of 2 were simulated (see Fig. 1B). A single substantial shift should be detected by the MMS-SMW analysis from small to large time windows. Such events have been documented for several ecosys-

tems in the North Pacific and in the North Sea (Hare & Mantua 2000, Reid et al. 2001).

**Case 3: cyclical variability.** Fifty time series with random temporal fluctuations of magnitude ranging from 0 to 1 (arbitrary unit) and a cyclical variability of magnitude 1 were simulated (see Fig. 1C). Many temporal discontinuities should be detected at times corresponding to the maximal local slope of the sinusoidal curve. This cyclical variability is sometimes associated with shifts in some upwelling ecosystems (e.g. sardine/anchovies oscillations) (Chavez et al. 2003).

**Case 4: episodic event.** Fifty time series with random temporal fluctuations of magnitude ranging from 0 to 1 (arbitrary unit) and an episodic event of magnitude 1 were simulated (see Fig. 1D). Two temporal discontinuities should be detected at times corresponding to the beginning and the end of the episodic event. The discontinuity should be detected at small time windows. Such an event was documented in the North Sea for plankton ecosystems (Edwards et al. 2002, Beaugrand & Ibanez 2004).

### Influence of the temporal autocorrelation on MMS-SMW analysis

Temporal autocorrelation can have a major influence on the procedure we present. Temporal autocorrelation can strongly increase the occurrence of false AESs. One way to overcome this issue could be to use the technique on detrended data. However, detrending a time series is not a straightforward step. Part of the signal related to the shift is often removed with the long-term trend (Beaugrand & Reid 2003). This issue has been detected, for example, in the case of singular spectrum analysis or in polynomial regression (Beaugrand et al. 2003). We therefore chose to use the technique on data that were temporally autocorrelated, knowing that this might affect the technique we present. However, to understand how MMS-SMW analysis can be influenced by autocorrelation, we designed 3 theoretical cases. For each type of situation, 50 time series of 100 regularly spaced time intervals corresponding to 100 hypothetical years were simulated and corresponded to year-to-year changes in 50 hypothetical species. The 3 cases were as follows (see Fig. 2):

**Case 5: very strong temporal autocorrelation.** Fifty time series were constructed with a linear trend of magnitude 100 (arbitrary unit) and random temporal fluctuations of magnitude 25.

**Case 6: strong temporal autocorrelation.** Fifty time series with a linear trend of magnitude 100 (arbitrary unit) and random temporal fluctuations of magnitude 50.

**Case 7: moderate temporal autocorrelation.** Fifty time series with a linear trend of magnitude 100 (arbitrary unit) and random temporal fluctuations of magnitude 100.

The MMS-SMW analysis was then applied on simulated time series corresponding to the 3 cases. We calculated the autocorrelograms (Legendre & Legendre 1998) and the associated confidence interval of 95 % for each simulated time series (Cases 5–7). The Box-Jenkins (Box & Jenkins 1976) autocorrelation function (ACF) modified by Chatfield (1996) was used. Note that the classification of the strength of the temporal autocorrelation (very strong, strong or moderate) is here arbitrary, with all time series from Case 5 to 7 having a minimum autocorrelation of order 12, which represents a very strong autocorrelation.

#### **Comparison of the temporal autocorrelation of simulated data with actual time series**

Autocorrelograms were built for both simulated and observed time series. We used simulated data corresponding to Case 5 (very strong autocorrelation) but on only 50 regularly spaced time intervals. This number of intervals was chosen to correspond to the exact number of years present in the observed time series (1958 to 2007) to allow us to compare the ACF of each variable in the same figure (Fig. 3).

#### **Effect of the statistical threshold on MMS-SMW analysis**

The MMS-SMW analysis was applied on the 50 simulated time series corresponding to Case 5 (very strong autocorrelation) using statistical thresholds of 5%, 1% and 0.5% (Fig. 4). This analysis was performed to examine to what extent the influence of autocorrelation on the occurrence of false AES can be alleviated by using a more conservative statistical threshold in the MMS-SMW analysis.

#### **Correlation analyses**

Relationships between long-term changes in the planktonic groups and hydro-climatic variables were investigated by linear correlation analysis. Probabilities were calculated with consideration of temporal autocorrelation (Pyper & Peterman 1998). The temporal ACF was calculated to allow an adjustment of the actual degree of freedom (Beaugrand et al. 2009).

All methods used in the present study were programmed using the MATLAB language.

## **RESULTS**

### **Theoretical examples to understand how to interpret results from MMS-SMW**

We examined 4 theoretical cases often encountered in the field to explain how the MMS-SMW analysis works and how it should be interpreted (Fig. 1). In Case 1, we applied the technique on 50 time series that only exhibit random temporal fluctuations (Fig. 1A). Although some significant discontinuities were found, no clear patterns emerged, and <5% of the 50 time series (or theoretical species) considered in this analysis (i.e. a maximum of 2.5 at a given time) exhibited a significant discontinuity ranging from small to large time windows at the classical statistical threshold of 5%. In Case 2, the simulated shift was detected, and nearly all time series (or theoretical species) exhibited a stepwise change at Time 50 (Fig. 1B). Other significant discontinuities found at other times were negligible and attributed to the effect described in Case 1. The discontinuity was less accurately detected using larger time windows. In Case 3, we found significant discontinuities corresponding to the maximum local slopes found along the sinusoidal curves (Fig. 1C). These discontinuities concerned many time series (or theoretical species) and were especially strong at larger time windows. Periods corresponding to both minima and maxima in the curves did not exhibit any AES. In Case 4, the technique identified well the simulated episodic event (Fig. 1D). Both the beginning and the end of the simulated episodic event were detected at small time windows in contrast to the simulated AES in Case 2, which was detected using all time windows.

### **Influence of the temporal autocorrelation on the MMS-SMW analysis**

The influence of the temporal autocorrelation on the frequency of false discontinuities was investigated. As expected for simulated time series, we found that temporal autocorrelation can drastically increase the number of false detections (Fig. 2). However, the analyses revealed how temporal autocorrelation affects the MMS-SMW analysis, showing that its signature on the diagram takes the form of a horizontal pattern (Fig. 2A). Temporal autocorrelation

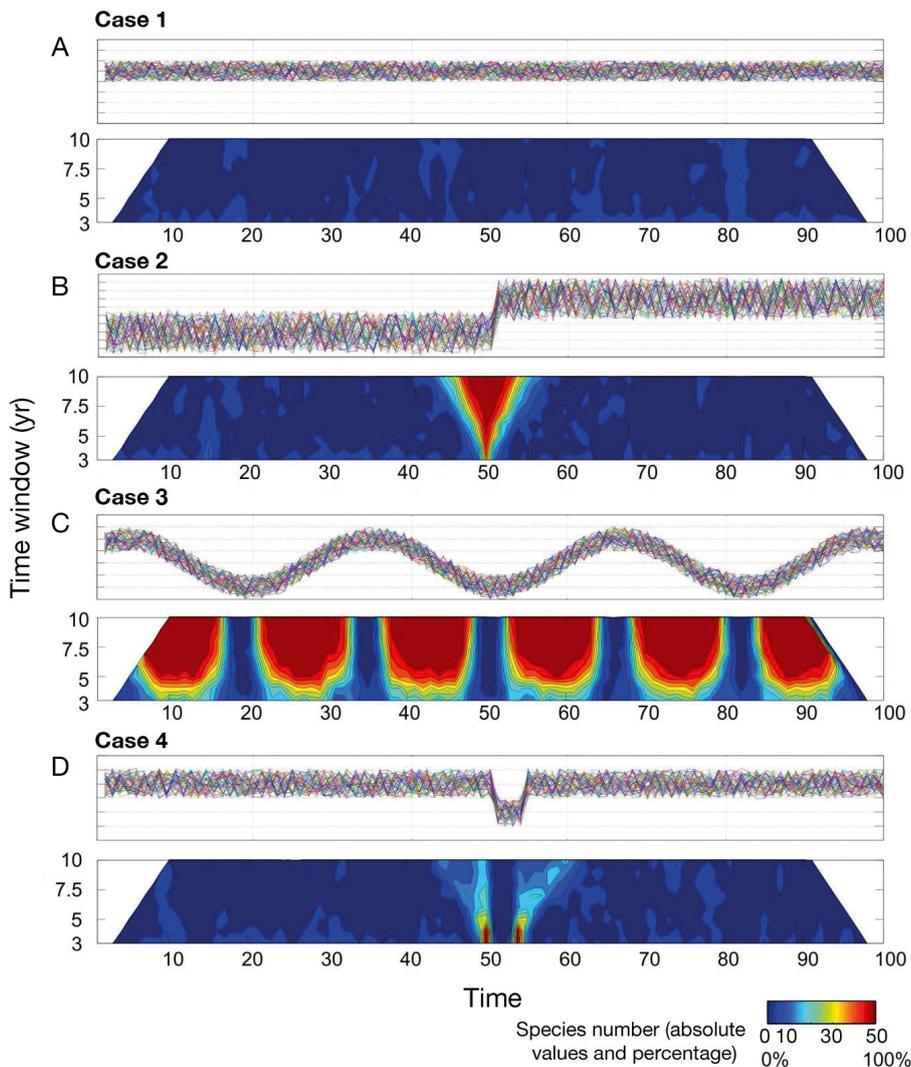


Fig. 1. Detectability principles of the technique MMS-SMW. Simulated time series and corresponding results from MMS-SMW in 4 types of situations. No temporal autocorrelation was introduced in the simulated time series. For each type of situation, 50 time series of 100 regularly spaced time intervals corresponding to 100 hypothetical years were simulated and corresponded to year-to-year changes in 50 hypothetical species (upper panels). MMS-SMW was then applied in each case and results shown in the lower panels. (A) Case 1: random fluctuation. Time series with random temporal fluctuations between 0 and 1. (B) Case 2: abrupt ecosystem shift. Time series with random temporal fluctuations of magnitude between 0 and 2.5 (arbitrary unit) and a discontinuity of 2. (C) Case 3: cyclical variability. Time series with random temporal fluctuations of magnitude between 0 and 1 (arbitrary unit) and a cyclical variability of magnitude 1. (D) Case 4: episodic events. Time series with random temporal fluctuations of magnitude between 0 and 1 (arbitrary unit) and an episodic event of magnitude 1

was more perceptible at larger time windows, where the amount of false detections was important (>50% of all time series). In areas of the diagram corresponding to smaller time windows, the number of false detections was much lower, representing only 10% of all time series. When temporal autocorrelation decreased, the number of false detections rapidly diminished from ~20% in Case 6 (Fig. 2B) to ~10% in Case 7 for large time windows (Fig. 2C). At smaller time windows, the percentage became negligible (~5%). The autocorrelograms were assessed for each time series simulated in Cases 5 to 7 (Fig. 2D) and showed the strength of the autocorrelation in all the simulated time series. Temporal autocorrelation was significant up to ~30 lags for Case 5, ~28 lags for Case 6 and ~12 lags for Case 7. Such extreme temporal autocorrelations are not frequently observed in the field, even for biological data.

We calculated the ACF of each observed time series used in the present study and compared them to time series simulated in Case 7 (Fig. 2). All the observed plankton and hydro-climatic time series had in general much lower temporal autocorrelation than simulated time series (Case 7). The observed time series with the strongest autocorrelation was the NHT anomalies (Fig. 3). To be conservative and knowing that the observed time series had smaller autocorrelations compared to Case 5, we examined the potential effect of the statistical threshold on the MMS-SMW analysis (Fig. 4). The effect of temporal autocorrelation on false detections was removed rapidly when the statistical threshold became more conservative. The persistence of the horizontal pattern constitutes a clear indication of the presence of autocorrelation. Although the influence of autocorrelation on the

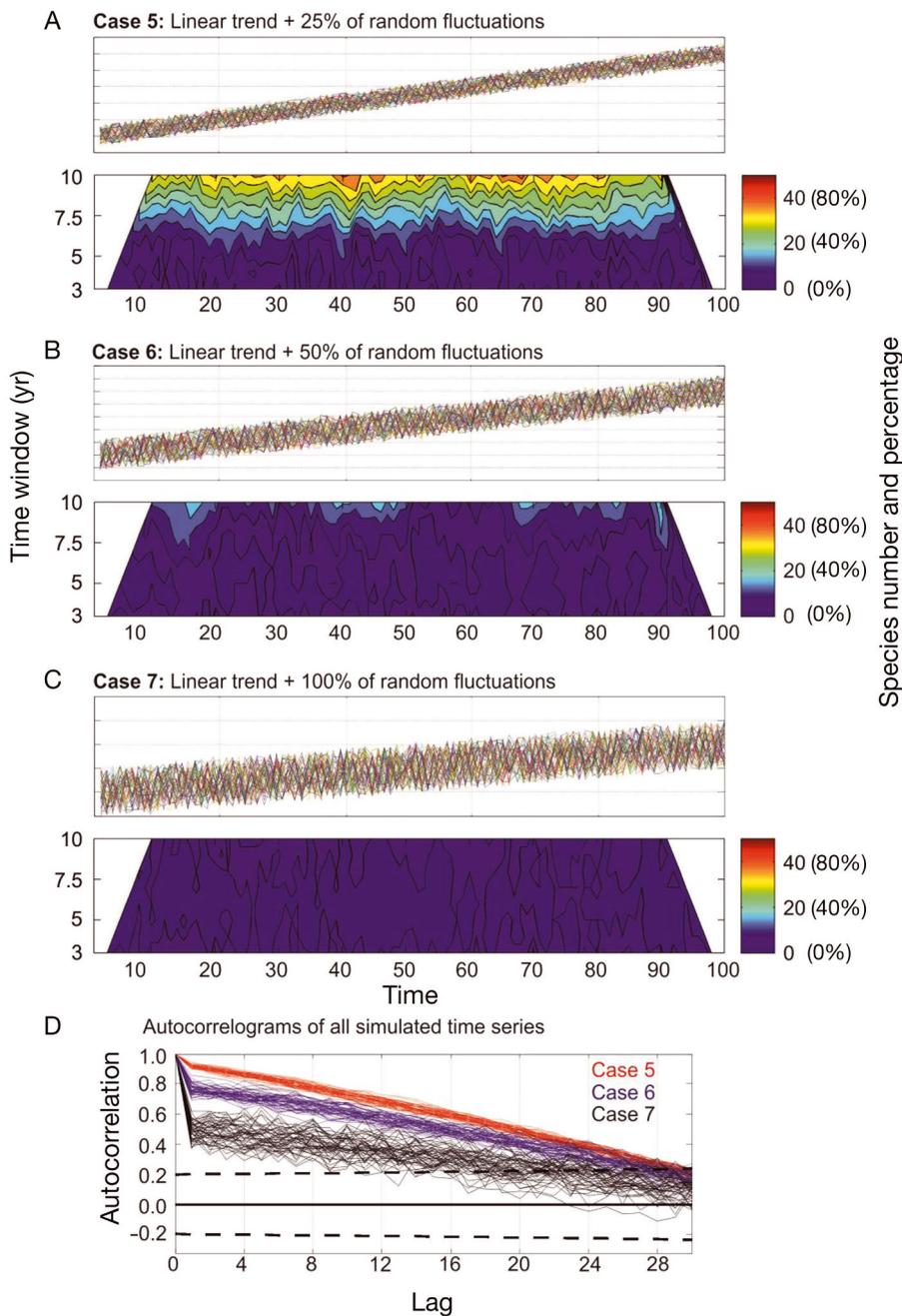


Fig. 2. Effect of temporal autocorrelation on MMS-SMW. Simulated time series and corresponding results from MMS-SMW in 3 types of situations. For each type of situation, 50 time series of 100 regularly spaced time intervals corresponding to 100 hypothetical years were simulated and corresponded to year-to-year changes in 50 hypothetical species. MMS-SMW was then applied in each case. (A–C) Time series with a linear trend of magnitude 100 (arbitrary unit) and random temporal fluctuations of magnitude (A) 25, (B) 50 or (C) 100 (upper panel) and corresponding results of the MMS-SMW analysis (lower panel). (A) Case 5: very strong temporal autocorrelation. (B) Case 6: strong temporal autocorrelation. (C) Case 7: moderate temporal autocorrelation. (D) Autocorrelograms of all simulated time series for Case 5 (red), Case 6 (blue) and Case 7 (black). The horizontal black line indicates the line of zero correlation. The dashed black lines denote the confidence interval of 95%. Autocorrelations outside this interval are significant. The classification of the strength of the temporal autocorrelation (very strong, strong or moderate) is here relative because all time series from Cases 5 to 7 had a minimum autocorrelation of order 12

MMS-SMW analysis can be strong, its effect is indicated by the presence of a horizontal pattern on the diagram and can be alleviated by selecting a more conservative threshold. However, we caution that an overly conservative threshold might decrease the sensitivity of the technique and have an adverse effect. Even in Case 5 (very strong autocorrelation), the maximum proportion of time series that exhibited a significant discontinuity was <10% at the statistical threshold of 0.5%.

### Long-term changes in diatoms

Long-term changes in the first principal component (PCA on diatoms), representing 29.20% of the total variance, showed first a decrease from 1958 to 1982, particularly pronounced at the end of the 1960s (Fig. 5A). Then, 2 stepwise increases occurred at the beginning of the 1980s and the end of the 1990s. The eigenvectors indicated that the first component reflected an increase in the abundance of the 19 dia-

toms, such as *Asterionella glacialis* and *Paralia sulcata* (Appendix 1). Long-term changes in the second component (11.73% of the total variance) showed a stepwise change at the end of the 1980s (Fig. 5B).

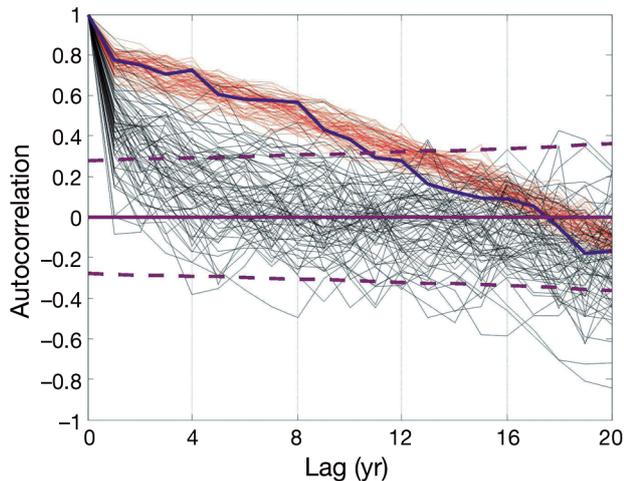


Fig. 3. Autocorrelograms of all simulated time series corresponding to Case 7 and observed CPR (73 time series) and hydro-climatic time series (4 time series). The 50 simulated time series were shortened to 50 regularly spaced intervals to correspond to the length of the observed time series (1958 to 2007). In red: autocorrelation functions (ACFs) of the 50 simulated time series corresponding to Case 7; in black: ACFs of the planktonic and hydro-climatic time-series; in blue: ACF of NHT anomalies. The purple line is the line of zero correlation. The dashed purple lines indicate the confidence interval of 95%. Autocorrelations outside this interval are significant

Only 5 species were related to this component. For the group of *Chaetoceros* and *Odontella regia*, negatively related to the second component, the second component indicated a decrease in abundance after the stepwise change, while for *Rhaphoneis amphicerus* and *Gyrosigma*, positively related to the component, this represented an augmentation in abundance (Appendix 1). While the first component was significantly correlated positively to the AMO index, the second component was positively correlated to annual SST and to a lesser extent the winter NAO index (Table 1). Although the correlation between the second component and NHT anomalies was high ( $r = 0.71$ ), the probability was not significant because of the strong autocorrelation of NHT. However, the correlation makes sense as SST and the second component were significantly correlated.

The MMS-SMW analysis detected well the influence of the cold-biological episodic event in the North Sea between 1978 and 1982 (Edwards et al. 2002), when between 8 and 12 species or taxa exhibited a significant discontinuity (24 and 36% of the diatoms) (Fig. 5C). The 2 discontinuities were only detected for small time windows (up to 5 yr), which indicates that the abrupt shift was more an episodic event than an AES with strong temporal persistence. A major AES was found in 1967 when >50% of the diatom species of taxa exhibited a pronounced decrease. Another discontinuity was identified around 1997 (1996 to 1998), reflecting a pronounced increase in the abundance of species (especially for species

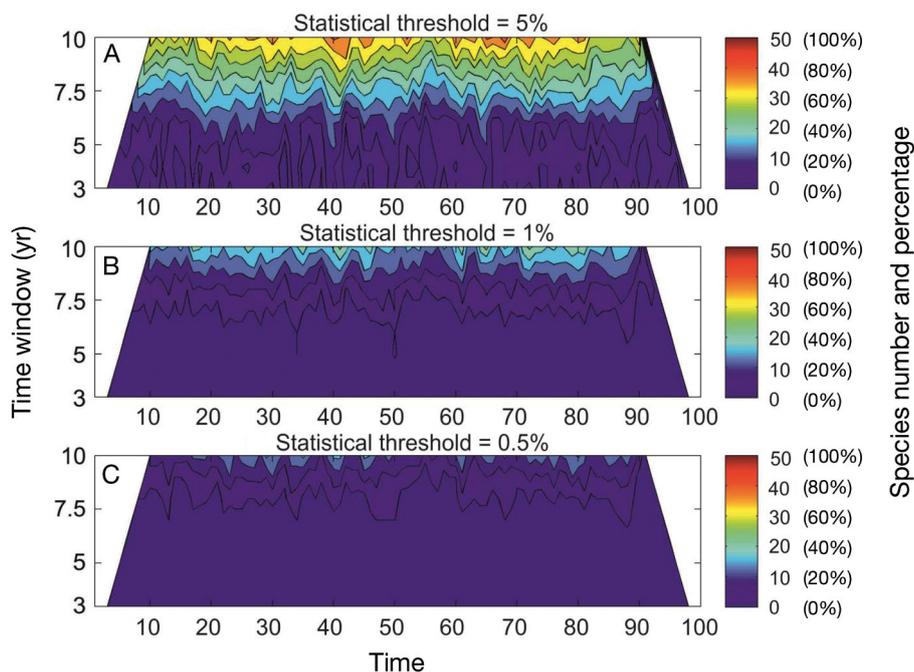


Fig. 4. Influence of the statistical threshold used in MMS-SMW when time series are strongly autocorrelated. We used simulated time series corresponding to Case 5 (see Fig. 2A), which had very strong autocorrelation (see Fig. 2D), with a statistical threshold of (A) 5%, (B) 1% and (C) 0.5%. The effect of temporal autocorrelation was in large part removed by the reduction in the statistical threshold

related to the first component) and a decrease for *Rhaphoneis amphiceros* and to a lesser extent the genus *Gyrosigma*. More than 50% of the diatoms were impacted by this pronounced change. While we

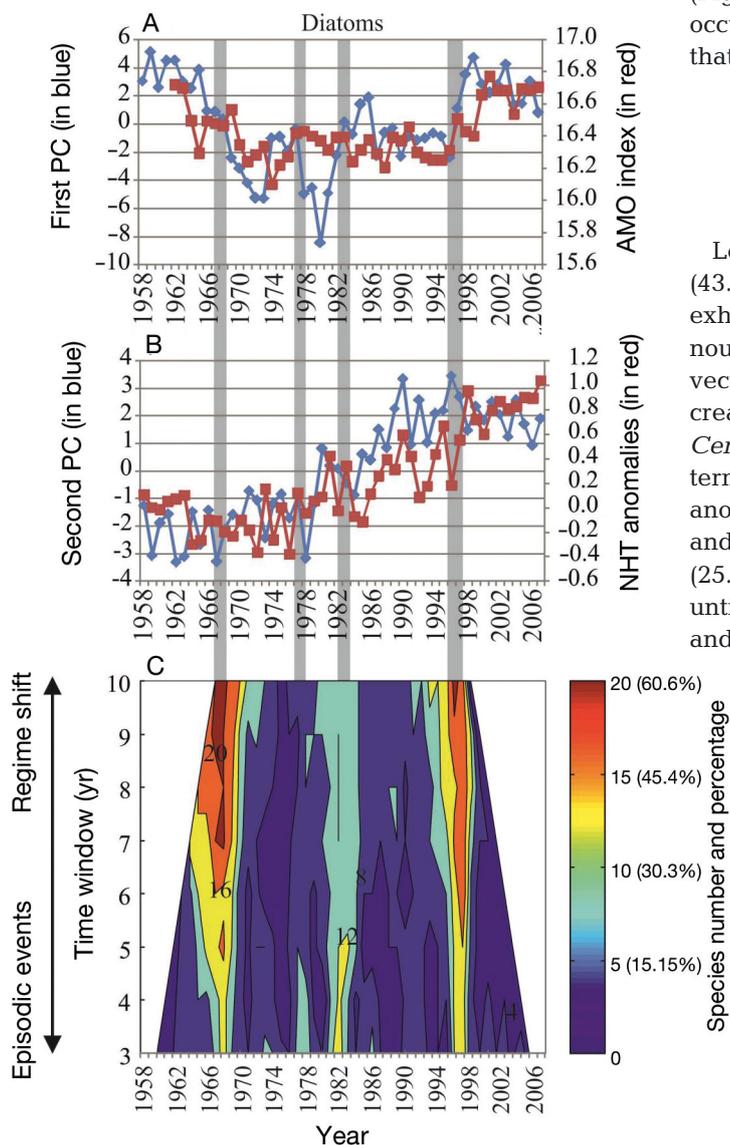


Fig. 5. Long-term changes in diatoms (33 species or taxa) in the North Sea for the period 1958 to 2007. (A) Long-term changes in the first principal component (29.2% of the total variance) in relation to the AMO index. (B) Long-term changes in the second principal component (11.73% of the total variance) in relation to NHT anomalies. The hydro-climatic indices were selected on the basis of Table 1. (C) Number of diatom species (as actual number and as percentage) or taxa that show a significant discontinuity ( $p \leq 0.05$ ) for a given half-window and year. The grey bars indicate important (significant) discontinuities detected by MMS-SMW. When the shift was significant for  $>1$  yr, the bar was placed at the middle of the stepwise change or at the location when the discontinuity was detected for a large number of time windows. Some significant but less important discontinuities are not indicated when they are not clearly identified in the first 2 principal components

provide the year of change, the shift was not completed in a single year but rather over a period of several years (Fig. 5). The new regime revealed by the second principal component at the end of the 1980s (Fig. 5B) was not the result of a rapid shift that occurred in a single year but was the result of a shift that began at the beginning of the 1980s.

### Long-term changes in dinoflagellates

Long-term changes in the first principal component (43.11% of the total variance; PCA on dinoflagellates) exhibited a slight decrease until 2000, when a pronounced increase was detected (Fig. 6A). The eigenvectors revealed that the component reflected a decrease in the abundance of dinoflagellates such as *Ceratium tripos* and *C. furca* (Appendix 1). The long-term changes were negatively correlated to NHT anomalies and to a lesser extent to the AMO index and SST (Table 1). The second principal component (25.75% of the total variance) showed an increase until 1989 with 2 phases of acceleration around 1974 and 1987 (Fig. 6B). After 1989, the values decreased.

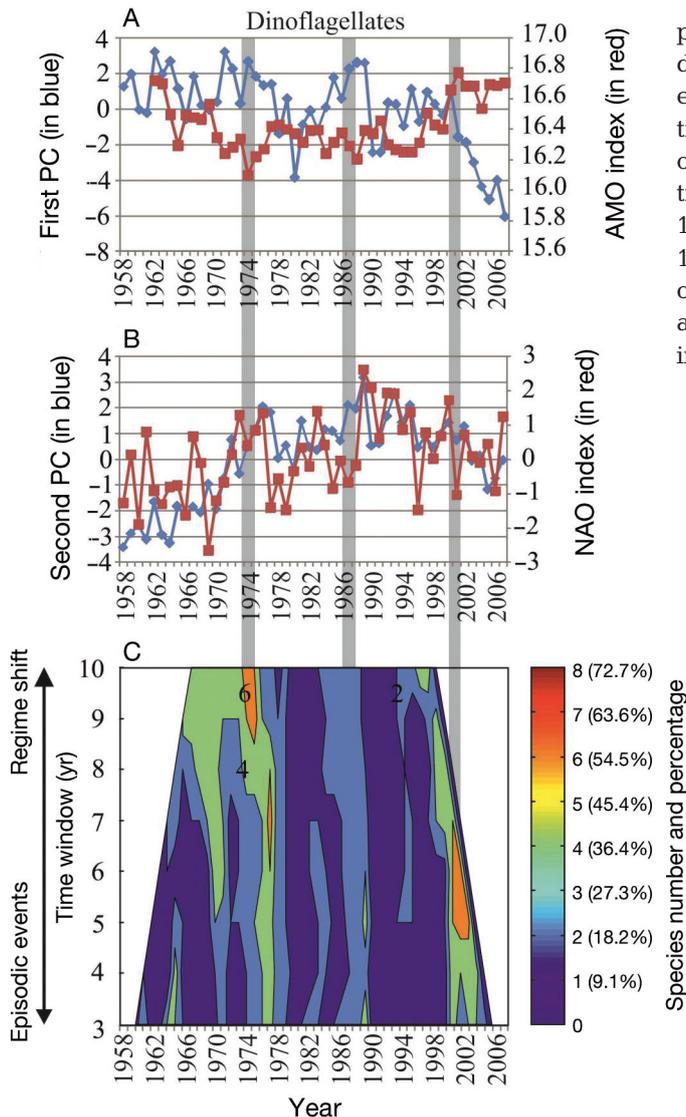
Such long-term changes reflected changes in small dinoflagellates such as *Gonyaulax* and were negatively correlated with changes in the abundance of *C. macroceros* (Appendix 1). The changes in the component positively covaried with the winter NAO index (Table 1). The MMS-SMW analysis detected an abrupt shift for dinoflagellates ca. 1975 ( $>50\%$  of species), a small shift (up to 36% of species) at the end of the 1980s and a more pronounced one between 1996 and 2003 (50% of species on average) (Fig. 6C). The cold-biological episodic event was also detected, concerning  $\sim 36\%$  of species, but the end of this event was less marked, probably indicating that some species did not recover.

### Long-term changes in copepods

Long-term changes in the first principal component (27.96% of the total variance; PCA on copepods) exhibited an increase particularly pronounced around 1987 (Fig. 7A). The eigenvectors indicated that these changes were positively correlated to changes in the abundance of species such as *Corycaeus* and *Candacia armata* and nega-

Table 1. Correlations between the long-term changes in the first 2 principal components and hydro-climatic indices. SST: sea surface temperature; NAO: winter North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index; NHT: Northern Hemisphere Temperature (NHT) anomalies. Significant ( $p \leq 0.05$ ) correlations are indicated in **bold**. All probabilities were corrected for temporal autocorrelation. The probability of significance is indicated when correlation is high but not significant and when the probability is  $<0.1$

	SST	NAO	AMO	NHT
PC1 diatoms	0.31	-0.03	<b>0.53</b>	0.31
PC2 diatoms	<b>0.53</b>	<b>0.39</b>	0.06	0.71
PC1 dinoflagellates	<b>-0.42</b>	-0.09	-0.46	<b>-0.63</b>
PC2 dinoflagellates	0.21	<b>0.50</b>	-0.40	0.29
PC1 copepods	<b>0.82</b>	<b>0.46</b>	0.32	<b>0.78</b>
PC2 copepods	-0.01	-0.14	0.26	0.24
PC1 other holozooplankton	-0.14	0.03	-0.11	0.09
PC2 other holozooplankton	-0.37	-0.31	-0.15	-0.55
PC1 meroplankton	<b>0.59</b>	0.28	0.41	0.56
PC2 meroplankton	<b>-0.44</b>	-0.03	-0.30	-0.45



tively correlated to *Calanus finmarchicus* and *Oithona* spp. (Appendix 1). The long-term trend was remarkably correlated positively to SST, NHT anomalies and to a lesser extent the NAO (Table 1). The second principal component clearly identified the cold-biological episodic event and 2 warm events in the periods 1958–1960 and around 1990 (Fig. 7B). As the percentage of variance explained by this component was similar to the first (27.15% of the total variance), many species showed variations (negatively) correlated to the component (e.g. the group *Parapseudocalanus* and *Temora longicornis*) (Appendix 1). No hydro-climatic factors were related to this component (Table 1). The MMS-SMW analysis clearly detected the cold-biological episodic event, but the end of the event was more intense, concerning larger time windows and therefore indicating both the end of the cold-biological episodic event and the initiation of the AES detected at the beginning of the 1980s (Fig. 7C). A larger shift was observed from 1990 to 2000, reflecting more a long-term adjustment of the community than an abrupt shift with 2 accelerations around 1990 and 1999. All shifts detected involved between 40% and 50% of copepods.

#### Long-term changes in other holozooplankton

Long-term changes in the first principal component (33.19% of the total variance; PCA on other holozooplankton, i.e. other than copepods) identified a strong event that appeared from 1959 to 1962 (Fig. 8A). The intensity of the event masked a sustained decrease noticeable around 1983. The eigenvectors revealed that

Fig. 6. Long-term changes in dinoflagellates (11 species or taxa) in the North Sea for the period 1958 to 2007. (A) Long-term changes in the first principal component (43.11% of the total variance) in relation to the AMO index. (B) Long-term changes in the second principal component (25.75% of the total variance) in relation to the winter NAO index. The hydro-climatic indices were selected on the basis of Table 1. (C) Number of dinoflagellate species (as actual number and as percentage) or taxa that show a significant discontinuity ( $p \leq 0.05$ ) for a given half-window and year. Grey bars as in Fig. 5

taxonomic groups such as Gammaridea and species such as *Limacina retroversa* were significantly negatively correlated to the principal component (Appendix 1). No correlation was found between this principal component and hydro-climatic indices (Table 1). The second principal component (21.86% of the total variance) showed an event in 1961 and exhibited a pronounced increase around 1983 (Fig. 8B). Species related to this component belonged to the groups of Larvacea and Cumacea (positive correlation) and euphausiids (negative correlation) (Appendix 1). The long-term changes in this component were negatively correlated to NHT anomalies, but the probability was not significant after accounting for temporal autocorrelation (Table 1). The MMS-SMW analysis

detected a shift around 1974 involving 66.6% of the species and around 1982 for ~88% of the holozooplankton (excluding copepods; Fig. 8C). The examination of the components indicated even though the first shift appeared to be weak, the second was much more pronounced.

### Long-term changes in meroplankton

Long-term changes in the first principal component (37.59% of the total variance; PCA on meroplankton) exhibited the cold-biological episodic event of 1978 to 1982. The event separated a period characterised by lower values (before the event) to a period with values generally higher (after the event; Fig. 9A). The taxonomic groups related to the component were mainly echinoderms, decapods and fish larvae (positive correlation; Appendix 1). A positive correlation was found between the component and both SST and NHT anomalies (Table 1). Again, the strong autocorrelation of NHT anomalies makes the correlation not significant at the probability threshold of 0.05. The second principal component (28.79% of the total variance) revealed 2 periods of positive anomalies (1958–1976 and 1983–1997) and 2 periods of negative anomalies (1977 to 1982 and 1998 onward) (Fig. 9B). Larvae of bivalves and Cyphonautes were positively correlated to the component, whereas fish eggs were negatively correlated (Appendix 1). The second principal component was correlated negatively to SST and NHT anomalies (Table 1). The MMS-SMW analysis detected the shift associated to the cold-biological episodic event and a shift at the beginning of the 1980s, which involved 80% of the meroplankton species. A second shift starting at the end of the 1990s was observed for 60% of the meroplankton.

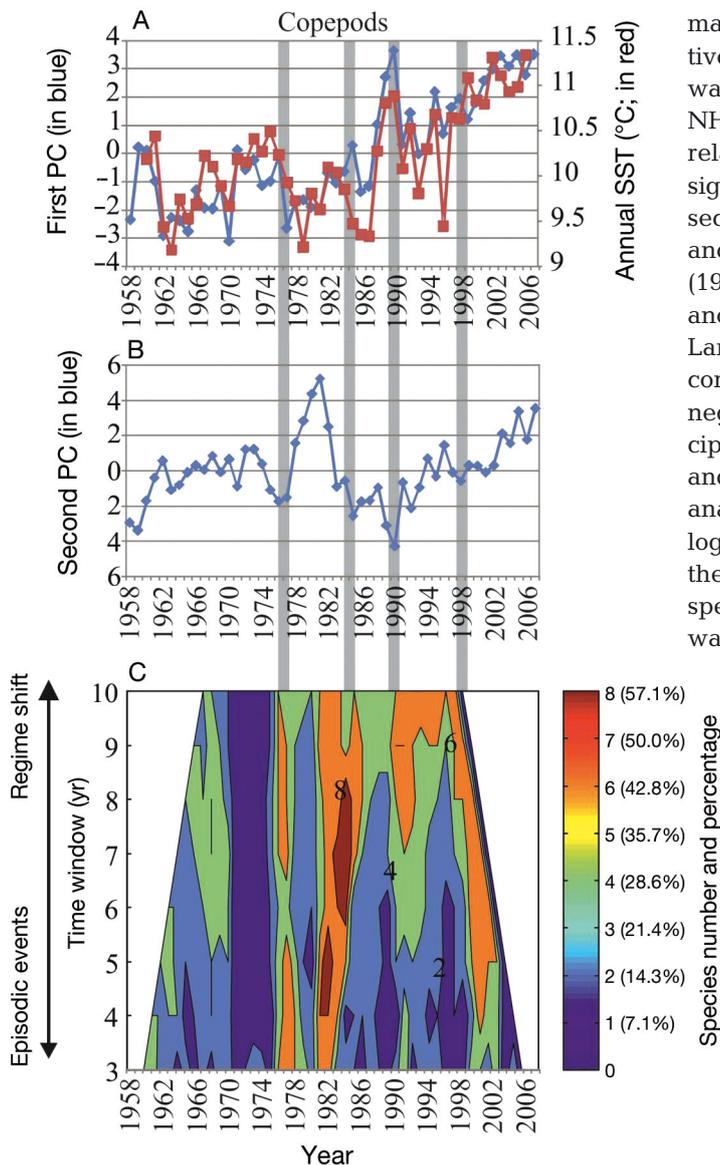


Fig. 7. Long-term changes in copepods (14 species or taxa) in the North Sea for the period 1958 to 2007. (A) Long-term changes in the first principal component (27.96% of the total variance) in relation to sea surface temperature. (B) Long-term changes in the second principal component (27.15% of the total variance). The hydro-climatic indices were selected on the basis of Table 1. (C) Number of copepod species (as actual number and as percentage) or taxa that show a significant discontinuity ( $p \leq 0.05$ ) for a given half-window and year. Grey bars as in Fig. 5

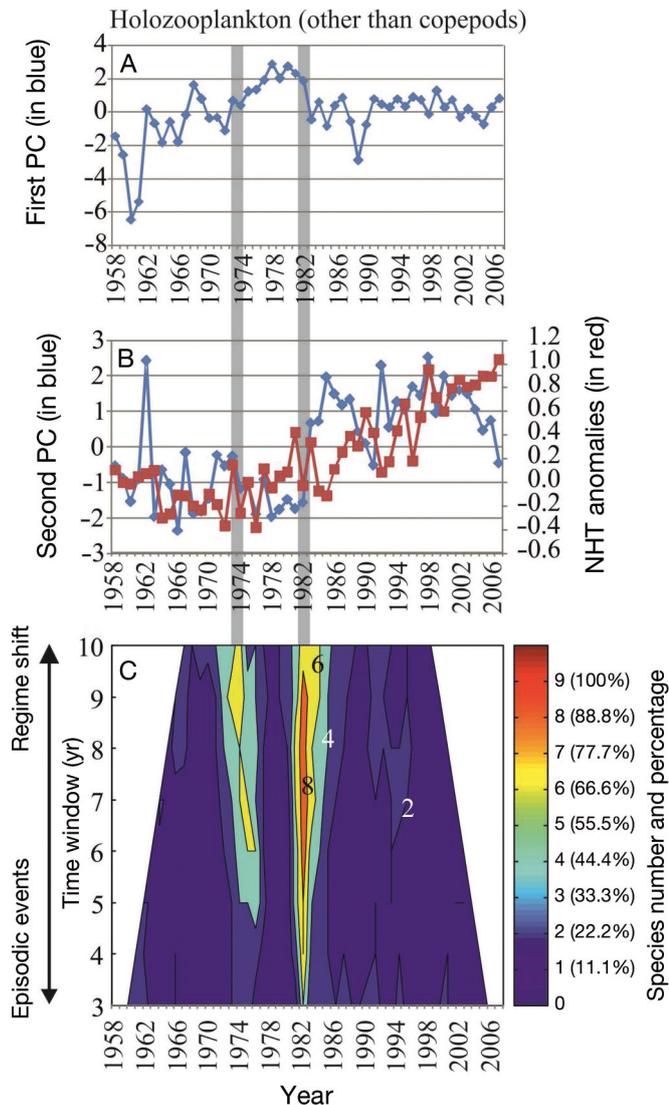


Fig. 8. Long-term changes in other holozooplankton (9 species or taxa) in the North Sea for the period 1958 to 2007. (A) Long-term changes in the first principal component (33.19% of the total variance). (B) Long-term changes in the second principal component (21.86% of the total variance) in relation to NHT anomalies. The hydro-climatic index was selected on the basis on Table 1. (C) Number of holozooplankton species (as actual number and as percentage) or taxa that show a significant discontinuity ( $p \leq 0.05$ ) for a given half-window and year. Grey bars as in Fig. 5

### MMS-SMW analysis for all plankton species

When applied to all plankton species, the MMS-SMW analysis detected the start of the cold-biological episodic event; a high number of species (~30% of all species) exhibited a significant discontinuity in 1977 for small time windows (Fig. 10A). The end of this event was detected in 1982, but the technique also in-

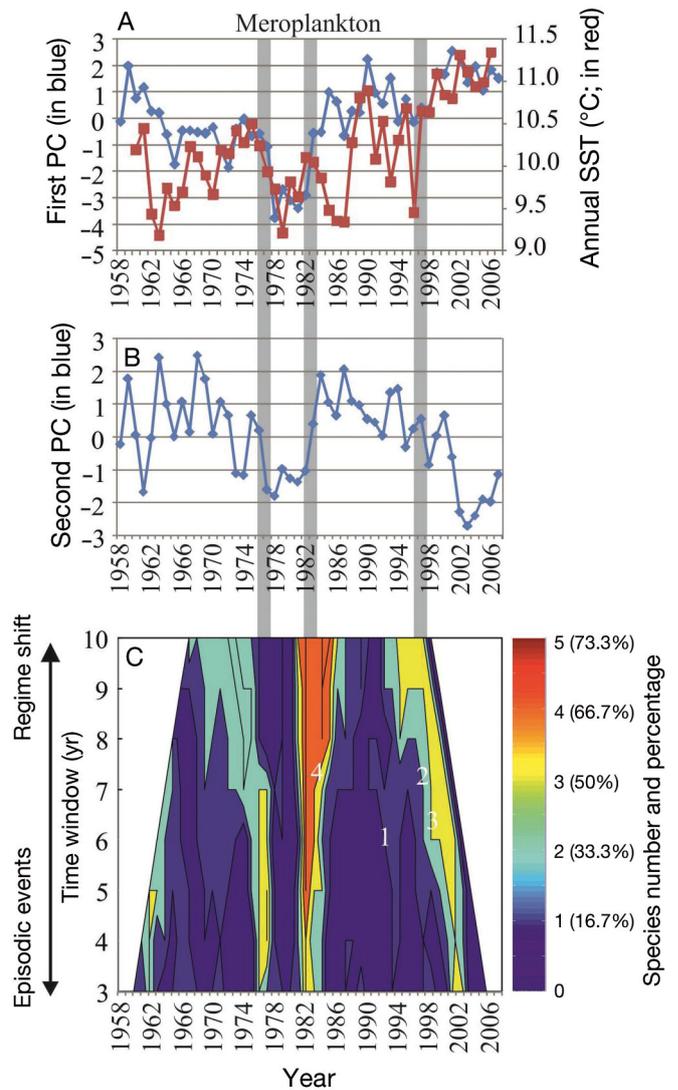


Fig. 9. Long-term changes in meroplankton (6 species or taxa) in the North Sea for the period 1958–2007. (A) Long-term changes in the first principal component (37.59% of the total variance) in relation to sea surface temperature. (B) Long-term changes in the second principal component (28.79% of the total variance). The hydro-climatic index was selected based on Table 1. (C) Number of holozooplankton species (as actual number and as percentage) or taxa that show a significant discontinuity ( $p \leq 0.05$ ) for a given half-window and year. Grey bars as in Fig. 5

dicated an AES between 1982 and 1985. Two other AESs were detected around 1968 and between 1996 and 2003, involving >40% of the species or taxa. Decreasing the probability of significance increased the accuracy of the timing of the shifts (1968, 1982 and 1996 to 1997), although the number of species presenting a significant discontinuity decreased by half when the probability equaled 0.01 and by a further 30% when the probability was fixed at 0.005 (Fig. 10).

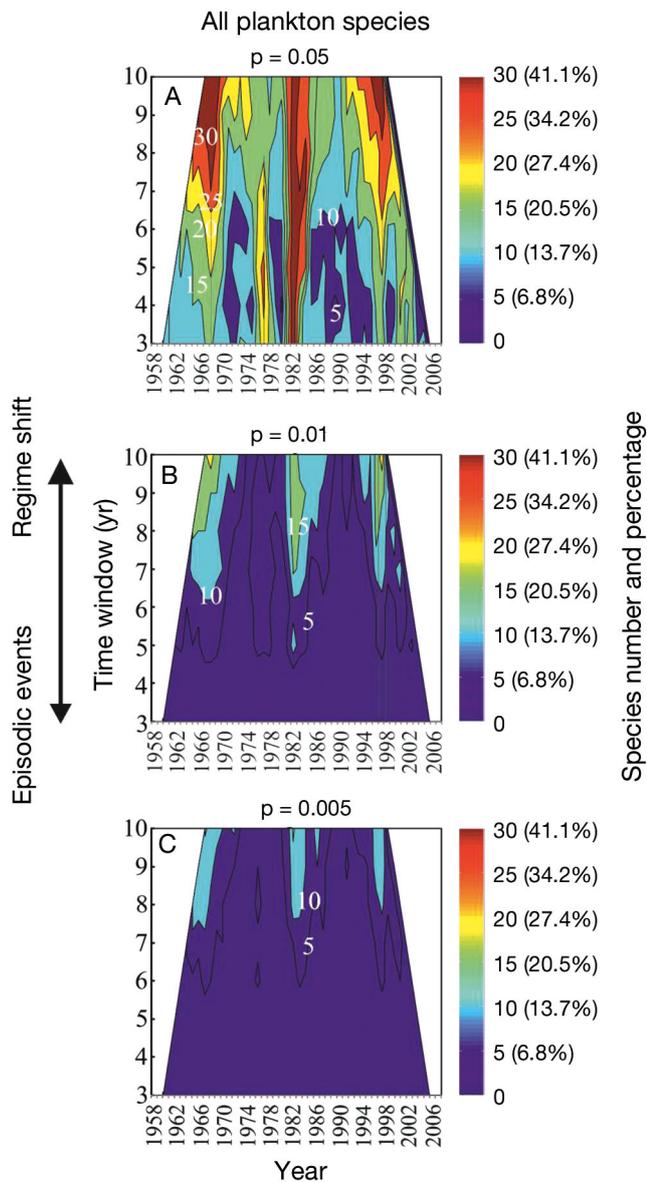


Fig. 10. Long-term changes in the whole plankton community (73 species or taxa) in the North Sea for the period 1958 to 2007 for a level of probability of (A) 0.05, (B) 0.01 and (C) 0.005

## DISCUSSION

### Methodological considerations

The issue of AES is complex and encompasses many issues: (1) definition, (2) detection, (3) quantification, (4) origin of shifts and (5) prediction (deYoung et al. 2008). It took a decade before Hare & Mantua (2000) and Reid et al. (2001) identified the Pacific and the North Sea AESs, respectively. The last shift (1996 to 2003) we detected in the present study also took a decade to be identified. Clearly, it is time to under-

take a more coordinated approach to the global monitoring of the oceans and to rapidly associate this monitoring to mathematical procedures of detection (Edwards et al. 2010, Goberville et al. 2011). However, the design and application of mathematical tools are highly dependent on the definition of an AES. DeYoung et al. (2004) proposed an operational definition of the term regime shift. They defined the term as a rapid and substantial change in the state of an ecosystem, the state lasting longer than the transitional period. Such an operational definition was also used by Yasunaka & Hanawa (2002). However, it was obvious that actual stable states might not really exist in plankton ecosystems and that regime shift could perhaps be better envisioned as stepwise changes or transitional phase shifts. This led Beaugrand et al. (2008) to prefer the term AES and to characterise 'stable' states and transitional periods by their variance signature. 'Stable' states were detected by their low levels of temporal variance and transitional periods by their higher levels of temporal variance. The significant temporal discontinuities we detected by MMS-SMW analysis in the present study correspond approximately to the middle part of a transitional period.

Many techniques can be applied to detect a temporal discontinuity (Beaugrand 2004b, Mantua 2004, Rodionov 2004). In the present paper, we based our approach on Webster's technique to identify and quantify the magnitude of an abrupt shift (Cornelius & Reynolds 1991). Webster's technique was criticised because it was intuitive that the results might change as a function of the selected time window (Cornelius & Reynolds 1991, Beaugrand 2004b). To take this potential drawback into account, we applied the technique using a full range of time windows prior to and after a given year, i.e. a time window between 6 and 20 yr around each year. Therefore, we identified years when changes accelerate and examined how the results were altered by the temporal scale. An AES identified only for small time windows suggests that the shift is an episodic event (Edwards et al. 2002), whereas an identification based on small to large time windows reflects an AES with strong temporal persistence (Yasunaka & Hanawa 2002, deYoung et al. 2008). Application of MMS-SMW to actual plankton time series has shown that our technique can detect shifts at the beginning, middle and end of a time series (Figs. 5–9). However, it should be noted that shifts cannot be identified toward the edges of the times series at larger time windows.

The technique was also transformed to examine the effect of a shift at the community level (Figs. 5–

10). The Kruskal-Wallis test we applied to compare 2 temporal windows was aimed to detect a change in the mean state. The MMS-SMW analysis compares means between time periods at the species level. Other techniques focussing on the variance (Beaugrand et al. 2008) should be used to complement the technique we present. Because ecosystems vary at a large range of scales and exhibit an endless number of situations and trajectories (Haury et al. 1978, McGowan 1990, Levin 1992), it is important to jointly use different approaches to better appreciate the mechanisms and the drivers of long-term ecosystem changes.

The most important problem with the MMS-SMW analysis, but in fact with most (not to say all) statistical techniques, is the impact of temporal autocorrelation on the results (Montgomery 1991). It has been shown that the detection and the magnitude of a shift can be influenced by temporal autocorrelation (Rudnick & Davis 2003). Autocorrelation has an effect on the procedure we present (see Figs. 2–4). Its effect is to increase the probability of finding a shift where there is none, at a given probability threshold (Sokal & Rohlf 1995). Our analyses based on simulated data revealed that temporal autocorrelation creates a horizontal pattern (Fig. 2).

Here, we quantified an AES by the percentage of species having a significant temporal discontinuity at a threshold  $p = 0.05$ . We also examined whether the shift was still observed at a lower probability (Fig. 10). This was the case for all shifts detected at the levels  $p = 0.01$  and  $p = 0.005$ . Therefore, it is unlikely that the timing of the shift was affected by temporal autocorrelation. In contrast, the intensity of the shift was reinforced by autocorrelation (Fig. 10), but this effect was probably small in our study because many observed time series had an autocorrelation weaker than simulated time series that had a noticeable effect on the MMS-SMW analysis (Case 7 versus Case 5; Figs. 2–4). At small time windows, simulated time series based on very strong autocorrelation found less than ~10% of the time series that exhibited a shift, whereas the 3 abrupt ecosystem shifts we detected involved ~40% of the species. A local increase in the autocorrelation is likely to be detected during a phase transition (Carpenter & Brock 2006, Carpenter et al. 2011). This increase is part of the phenomenon and should not be confounded with the autocorrelation associated with the presence of a long-term trend.

Another aspect is related to multiple testing (Legendre & Legendre 1998). For each year, we performed a large number of Kruskal-Wallis tests. When

all plankton species were considered together (73 species or taxa; Fig. 10), this number was equal to 73 for each year and time window. Therefore, 3.65 false detections were expected for each year and time window at  $p = 0.05$ . Although there are a number of ways to correct the probability of significance for multiple testing (e.g. the Bonferroni correction), such a correction is too conservative (Legendre & Legendre 1998). We therefore made the choice to not correct for multiple testing. All AESs involved a change of at least 40% of the total species number (Fig. 10), which is ~11-fold higher than the number of significant discontinuities expected by chance alone.

### **Main abrupt ecosystem shifts in the North Sea during the period 1958 to 2007**

The PCAs were applied to visualise the long-term changes in the abundance of each taxon or species belonging to the 5 planktonic groups and the MMS-SMW analysis allowed the intensity of the shift to be quantified. The MMS-SMW analysis applied to all species showed 3 main AESs that impacted ~40% of all plankton species considered in the present study, and therefore, ~60% of the species did not exhibit a significant change (Fig. 10). To our knowledge, such a direct quantification of the North Sea AES has never been undertaken. The 3 AESs were associated with a shift in temperature (either regional, global or both), the AMO and to a lesser extent the NAO, indicating that hydro-climatic conditions exerted a strong influence on North Sea ecosystems (Table 1).

A first AES took place around 1968, when 40% of all the species exhibited a significant temporal discontinuity. This shift was mostly detected for phytoplankton species (see Figs. 5 & 6). As many analyses on AESs only focussed on zooplankton and fish (Reid et al. 2001, Beaugrand 2004b), this shift has been poorly documented. These biological changes coincided with changes in hydro-climatic forcing, persistent in time for both NHT anomalies and the NAO index and more episodic for SST and the AMO index (Edwards et al. 2013). Although it is difficult to explain this decline in the diatom assemblage, there was a significant change in the successional cycle of diatoms (particularly the dominant *Chaetoceros* genus) around this period (Fig. 5). During the early part of the 1960s seasonal cycle, *Chaetoceros* spp. were not only found in high abundance during the spring bloom but also contributed to a significantly large autumnal bloom (Edwards et al. 2001). In the Northeast Atlantic, significantly large autumnal

blooms were recorded each year from 1960 to 1967; thereafter, the autumnal bloom virtually disappeared. Although the mechanisms behind this successional change are unclear, the disappearance of the autumnal bloom certainly had a profound effect on the annual abundance of diatoms (Edwards et al. 2001).

A second AES was detected during the 1980s. The timing of the shifts was concentrated around the beginning (e.g. diatoms) and sometimes the end of the 1980s (e.g. dinoflagellates, copepods; Figs. 5–10). This second shift also involved ~40% of all species (Fig. 10). When all species were considered, the shift was detected earlier than results originally suggested (Reid et al. 2001). Beaugrand (2004b) stressed that the 1980s were a transitional period from a colder dynamic regime (1963 to 1979) to a much warmer dynamic regime (1990 onward), although a peak was detected around 1982 and 1988. This result was subsequently rediscovered using a multivariate analysis of the local variance (Beaugrand et al. 2008). The whole decade was characterised by a high level of variance, indicative of a phase transition (Carpenter & Brock 2006). The transitional period was also identified by means of PCA performed on both biotic and abiotic data in the Baltic Sea (Lindegren et al. 2010). The study analysed a total of 48 abiotic and biotic factors during the period 1979 to 2005 and showed pronounced ecosystem changes during the 1980s. Beaugrand et al. (2008) explained this shift by the northward movement of a critical thermal boundary (also termed a vulnerability hotspot), characterised by the annual isotherm 9 to 10°C, in the 1980s in the North Sea due to warming of sea temperatures. This annual isotherm is a proxy for the boundary between the Atlantic Polar and Atlantic Westerly Winds biomes (Longhurst 1998), and its movement was identified by the decline in the abundance of subpolar species (e.g. *Calanus finmarchicus* and the Atlantic cod *Gadus morhua*) and the concomitant increase in warm-temperate species. Prior to the shift, 75% of the North Sea had an annual thermal regime between 9 and 10°C. After the shift, only 20% kept this thermal regime, the remaining geographical cells having an annual sea surface temperature above 10°C (Beaugrand et al. 2008).

A third and newly identified AES was detected between 1996 and 2003 (Fig. 10). Weijerman et al. (2005) also suggested this shift, although their time series stopped in 2002. The shift was as strong as the second detected in the present study and also involved ~40% of the total number of species or taxa (Fig. 10). Such changes were also seen in NHT anom-

alies, suggesting that it could be a direct consequence of global climate change on North Sea ecosystems. This shift was detected in all planktonic groups with the exception of holozooplankton other than copepods (9 species or taxa; Fig. 8). It is therefore likely that the implications of this shift for the trophodynamics of marine ecosystems will be as great as the one that took place in the 1980s. Many changes have been reported in the plankton (Edwards et al. 2009) and in fish and seabirds between 1996 and 2003 (Frederiksen et al. 2006, Kirby et al. 2006, Luczak et al. 2011). A substantial decline in the abundance of lesser sandeels *Ammodytes marinus* was observed in 2003 and associated with a concomitant increase in the abundance of snake pipefish *Entelurus aequoreus* (Harris et al. 2007). Frederiksen et al. (2006) showed that in general, the decline in the abundance of lesser sandeels was associated with a reduction in their plankton preys. A pronounced reduction in the breeding success of seabirds (e.g. common guillemot *Uria aalge* and black-legged kittiwake *Rissa tridactyla*) has been associated with a decrease in the energetic content of sprat, an increase in snake pipefish (much less energetic) associated with a decrease in the abundance of lesser sandeel and the reduction in the size of lesser sandeel (Wanless et al. 2004, 2005). The average size of sandeels declined by 11 mm for 0-group and 19 mm for mostly 1-group species from 1973 to 2002. Wanless et al. (2004) estimated that this decline corresponded to a reduction of 40% in energy content.

### Mechanisms and processes leading to abrupt ecosystem shifts

Processes and mechanisms leading to AESs in the North Sea remain difficult to identify and to understand. Some processes leading to AESs have been clearly identified in lakes and some marine ecosystems (Nyström et al. 2000, Scheffer & van Nes 2004, Scheffer 2009). When the system is controlled by keystone species, such as in seaweed-structured ecosystems (Carpenter 1990), or engineer species, such as in coral-dominated ecosystems (Nyström et al. 2000), alternative stable states are relatively well identified (Scheffer & van Nes 2004, Scheffer 2009). Causes of AESs in these systems originate in large part from human activities. For example, algal overgrowth in Caribbean coral reefs is mainly attributed to (1) nutrient loading, which stimulates algal growth, and (2) overfishing that reduces the number of herbivorous fish that control algal proliferation

(Nyström et al. 2000). When the herbivore regulating the system is a sea urchin (e.g. *Diadema antillarum* in some Caribbean coral reefs), the decline of its population due to a pathogen can lead to the same alternative stable state (Nyström et al. 2000). Other similar mechanisms have been invoked to explain trophic cascades caused by overfishing and alternative stable states in kelp forest ecosystems (Scheffer & van Nes 2004, Frank et al. 2005, Casini et al. 2009). However, how can we explain climate-induced AESs such as those observed in the Pacific Ocean (Hare & Mantua 2000), in the North Sea (Reid et al. 2001, Weijerman et al. 2005) and in our study?

The new shift we identified in the present study occurred during the period from 1996 to 2003, at a time of a major discontinuity in the intensity of warming (Levitus et al. 2009, Raitos et al. 2010, Reid & Beaugrand 2012). Reid & Beaugrand (2012) showed a pronounced climate-induced shift in temperature over all continental shelves, a warming that was particularly intense in the north-eastern part of the North Atlantic and its adjacent seas. This first effect of temperature through the thermal niche of a species is deterministic. However, when a community reassembles, interspecific relationships (e.g. predation, grazing, competition, parasitism, disease) within the community are perturbed, which in turn leads to a second alteration (Parmesan & Matthews 2006). This biotic modification, which can lead to a trophic amplification (Kirby & Beaugrand 2009), is not easy to forecast because species interactions are numerous and exhibit complex tipping points. The part of the reorganisation related to interspecific relationships is in practice (or in the current state of our knowledge of the trophodynamics of pelagic ecosystems) unpredictable and represents the stochastic component of the climate-induced AES.

In the present study, we interpret long-term changes in plankton, primarily as a function of temperature. Temperature has a cardinal influence on many physiological and ecological parameters (Brown et al. 2004, Forster & Hirst 2012) and explains a large amount of variance in long-term planktonic changes (Aebischer et al. 1990, Helaouët & Beaugrand 2007, Beaugrand et al. 2008, Kirby & Beaugrand 2009). However, we are aware of other environmental parameters that may also alter planktonic communities: nutrients, light, bathymetry and dissolved oxygen, to name a few (Sverdrup 1953, Pörtner 2001, Sarmiento & Gruber 2006, Longhurst 2007, Helaouët et al. 2011). Mixed layer depth is also an important parameter for phytoplankton production (Sverdrup 1953, Behrenfeld 2010). Wind direction, by

its control of the distribution of some meroplankton species, might strongly affect recruitment of some benthic organisms (Dickson et al. 1988, Jolly et al. 2009). However, macroecological studies have generally found that temperature was the most important factor driving both spatial and temporal changes in plankton (Rutherford et al. 1999, Beaugrand et al. 2000, Rombouts et al. 2010, Reygondeau & Beaugrand 2011) and other systems (Lomolino et al. 2006).

We found that species did not react at the same time during an EAS and that some did not even change during phases of accelerating change (Figs. 5–10). The difference in timing we observed between and within planktonic groups has also been previously stressed (Beaugrand 2004b). The difference in timing was also obvious in the analysis performed by Lindegren et al. (2010). The timing of a shift rarely coincided from one trophic group to another. This was especially the case for plankton, benthic organisms and fish when the sequential *t*-test method of Rodionov (2004) is used. Weijerman et al. (2005), analysing a large amount of both biological (both CPR data and other datasets) and physical data, reached implicitly similar conclusions on the timing. Indeed, the small percentage of variance explained by the first components (46 biological time series, 44 % of the total variance for the first 3 components) indicated that only a small fraction of the biological parameters considered in their study exhibited the same trend.

The absence of synchrony between taxonomic groups can arise from the type of applied statistical techniques (Beaugrand 2004b). This should not be linked to the robustness of a method but to its nature. For example, a cluster analysis is expected to reveal a homogeneous time period, while an analysis of the local variance in a time series focuses on the temporal heterogeneity. Therefore, the timing revealed by such techniques is different. Similarly, the visual inspection of a principal component (or a time series) is also subjective and depends whether one looks at the beginning of the new regime, the end of the previous regime or the middle of the phase transition.

The absence of synchrony between species or taxonomic groups may also originate from the inner biological characteristics of taxonomic groups. Species of different taxonomic groups are likely to not react or be influenced by the same environmental factors. For example, diatoms are very sensitive to the degree of seasonal variability in temperature, while the annual temperature regime does not have a large influence on this group (Margalef 1978, Edwards & Richardson 2004, Beaugrand et al. 2010). Taxa such

as dinoflagellates and copepods are more influenced by the annual thermal regime (Margalef 1978, Beaugrand et al. 2010). Furthermore, species have different spatial distributions, different characteristics of the life cycle, life histories and turnover rates. Species likely to be influenced by temperature are species that have their northern or southern limits of distribution close to or in the North Sea (Beaugrand et al. 2008, Beaugrand 2009).

## CONCLUSIONS

We show that 3 main AESs occurred in the North Sea during the period 1958 to 2007. We document a new shift that took place during the period 1996–2003 and that probably constitutes the response of the plankton ecosystems to a substantial increase in global temperature in the north-eastern regions of the North Atlantic Ocean and its adjacent seas (Reid & Beaugrand 2012). All AESs coincided with significant changes in hydro-climatic forcing and had major consequences for the structure of the ecosystems (Figs. 5–10), despite only concerning 40% of the plankton species or taxa. The timing of the shift varied according to the planktonic group and even among species within a taxonomic group.

*Acknowledgements.* The present work was supported by the 'Centre National de la Recherche Scientifique' (CNRS) and the programme BIODIMAR. We thank the 3 anonymous referees for significantly improving an early version of the manuscript.

## LITERATURE CITED

- Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753–755
- Alheit J (2009) Consequences of regime shifts for marine food webs. *Int J Earth Sci* 98:261–268
- Batten SD, Clark R, Flinkman J, Hays G and others (2003) CPR sampling: the technical background, materials, and methods, consistency and comparability. *Prog Oceanogr* 58:193–215
- Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fish Oceanogr* 12:270–283
- Beaugrand G (2004a) Monitoring marine plankton ecosystems. I: Description of an ecosystem approach based on plankton indicators. *Mar Ecol Prog Ser* 269:69–81
- Beaugrand G (2004b) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262
- Beaugrand G (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res II* 56:656–673
- Beaugrand G, Ibanez F (2004) Monitoring marine plankton ecosystems. II: Long-term changes in North Sea calanoid copepods in relation to hydro-meteorological variability. *Mar Ecol Prog Ser* 284:35–47
- Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Glob Change Biol* 9:801–817
- Beaugrand G, Reid PC, Ibañez F, Planque P (2000) Biodiversity of North Atlantic and North Sea calanoid copepods. *Mar Ecol Prog Ser* 204:299–303
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Beaugrand G, Ibañez F, Lindley JA (2003) An overview of statistical methods applied to the CPR data. *Prog Oceanogr* 58:235–262
- Beaugrand G, Edwards M, Brander K, Luczak C, Ibañez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol Lett* 11: 1157–1168
- Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803
- Beaugrand G, Edwards M, Legendre L (2010) Marine biodiversity, ecosystem functioning and the carbon cycles. *Proc Natl Acad Sci USA* 107:10120–10124
- Behrenfeld MJ (2010) Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. *Ecology* 91: 977–989
- Box GEP, Jenkins GW (1976) Time series analysis: forecasting and control. Holden-Day, San Francisco, CA
- Brander KM (2007) Global fish production and climate change. *Proc Natl Acad Sci USA* 104:19709–19714
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789
- Carpenter RC (1990) Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Mar Biol* 104:67–77
- Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. *Ecol Lett* 9:311–318
- Carpenter SR, Cole JJ, Pace ML, Batt R and others (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079–1082
- Casini M, Hjelma J, Molinero J-C, Lövgren J and others (2009) Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc Natl Acad Sci USA* 106: 197–202
- Chatfield C (1996) The analysis of time series: an introduction. Chapman and Hall, London
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen MC (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221
- Cornelius JM, Reynolds JF (1991) On determining the statistical significance of discontinuities within ordered ecological data. *Ecology* 72:2057–2070
- Cury P, Shannon L, Shin YJ (2003) The functioning of marine ecosystems: a fisheries perspective. In: Sinclair M, Valdimarsson G (eds) Responsible fisheries in the marine ecosystem. FAO and CAB international, Rome, p 103–123
- deYoung B, Barange M, Beaugrand G, Harris R, Perry RI, Scheffer M (2008) Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol Evol* 23:402–409

- deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: data considerations. *Prog Oceanogr* 60:143–164
- Dickson RR, Kelly PM, Colebrook JM, Wooster WS, Cushing DH (1988) North winds and production in the eastern North Atlantic. *J Plankton Res* 10:151–159
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Edwards M, Reid PC, Planque B (2001) Long-term and regional variability of phytoplankton biomass in the North-east Atlantic (1960–1995). *ICES J Mar Sci* 58:39–49
- Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar Ecol Prog Ser* 239:1–10
- Edwards M, Beaugrand G, John AWG, Licandro P, McQuatters-Gollop A, Reid PC (2009) Ecological status report 2007/2008. The ecological status of the North Atlantic environment based on observations from the Continuous Plankton Recorder survey. SAHFOS Technical Report, 5. Sir Alister Hardy Foundation for Ocean Science (SAHFOS), Plymouth
- Edwards M, Beaugrand G, Hayes GC, Koslow JA, Richardson AJ (2010) Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends Ecol Evol* 25:602–610
- Edwards M, Beaugrand G, Helaouët P, Alheit J, Coombs SH (2013) Marine ecosystem response to the Atlantic Multi-decadal Oscillation. *PLoS ONE* 8:e57212
- Enfield DB, Mestas-Nunez AM, Trimble PJ (2001) The Atlantic Multidecadal Oscillation and its relationship to rainfall and river flows in the continental U.S. *Geophys Res Lett* 28:2077–2080
- Forster J, Hirst AG (2012) The temperature-size rule emerges from ontogenic differences between growth and development rates. *Funct Ecol* 26:483–492
- Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–1623
- Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J Anim Ecol* 75:1259–1268
- Goberville E, Beaugrand G, Sautour B, Tréguer P (2011) Evaluation of coastal perturbations: a new mathematical procedure to detect changes in the reference state of coastal systems. *Ecol Indic* 11:1290–1300
- Greve W (1994) The 1989 German Bight invasion of *Mugilgiaea atlantica*. *ICES J Mar Sci* 51:355–358
- Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog Oceanogr* 47: 103–145
- Harris MP, Beare D, Toresen R, Nottestad L and others (2007) A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. *Mar Biol* 151:973–983
- Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele JH (ed) *Spatial pattern in plankton communities*. Plenum Press, New York, NY, p 277–327
- Helaouët P, Beaugrand G (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar Ecol Prog Ser* 345: 147–165
- Helaouët P, Beaugrand G, Reid PC (2011) Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Prog Oceanogr* 91:217–228
- Hurrell JW, Yochanan K, Visbeck M (2001) The North Atlantic Oscillation. *Science* 291:603–605
- Ibanez F, Dauvin JC (1998) Shape analysis of temporal ecological processes: long-term changes in English Channel macrobenthic communities. *Coenoses* 13:115–129
- Jolly MT, Guyard P, Ellien C, Gentil F, Viard F, Thiébaud E, Jollivet D (2009) Population genetics and hydrodynamic modeling of larval dispersal dissociate contemporary patterns of connectivity from historical expansion into European shelf seas in the polychaete *Pectinaria koreni* (Malmgren). *Limnol Oceanogr* 54:2089–2106
- Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. *Proc R Soc Lond B Biol Sci* 276: 4095–4103
- Kirby RR, Johns DG, Lindley JA (2006) Fathers in hot water: rising sea temperatures and a Northeastern Atlantic pipefish baby boom. *Biol Lett* 2:597–600
- Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier, Amsterdam
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Levitus S, Antonov JI, Boyer TP, Locarnini RA, Garcia HE (2009) Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems. *Geophys Res Lett* 36:L07608
- Lindegren M, Diekmann R, Möllmann C (2010) Regime shifts, resilience and recovery of a cod stock. *Mar Ecol Prog Ser* 402:239–253
- Lindley JA, Roskell J, Warmer AJ, Halliday NC, Hunt HG, John AWG, Jonas TD (1990) Doliolids in the German Bight in 1989: evidence for exceptional inflow into the north sea. *J Mar Biol Assoc UK* 70:679–682
- Lindley JA, Williams R, Hunt HG (1993) Anomalous seasonal cycles of decapod crustacean larvae in the North Sea plankton in an abnormally warm year. *J Exp Mar Biol Ecol* 172:47–65
- Lomolino MV, Riddle BR, Brown JH (2006) *Biogeography*. Sinauer Associates, Sunderland, MA
- Longhurst A (1998) *Ecological geography of the sea*. Academic Press, London
- Longhurst A (2007) *Ecological geography of the sea*. Elsevier, Amsterdam
- Luczak C, Beaugrand G, Jaffré M, Lenoir S (2011) Climate change impact on Balearic shearwater through a trophic cascade. *Biol Lett* 7:702–705
- Mantua NJ (2004) Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to north pacific data. *Prog Oceanogr* 60:165–182
- Margalef R (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol Acta* 1: 493–509
- McGowan JA (1990) Species dominance-diversity patterns in oceanic communities. In: Woodwell GM (ed) *The earth in transition*. Cambridge University Press, Cambridge, p 395–421
- Mielke PW, Berry KJ, Brier GW (1981) Application of multiresponse permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. *Mon Weather Rev* 109:120–126
- Montgomery DC (1991) *Introduction to statistical quality control*. John Wiley & Sons, New York, NY
- Nyström M, Folke C, Moberg F (2000) Coral reef distur-

- bance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Parmesan C, Matthews J (2006) Biological impacts of climate change. In: Groom MJ, Meffe GK, Carroll CR (eds) *Principles of conservation biology*. Sinauer Associates, Sunderland, MA, p 333–360
- Pörtner H (2001) Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* 88:137–146
- Pyper BJ, Peterman RM (1998) Comparison of methods to account for autocorrelation analyses of fish data. *Can J Fish Aquat Sci* 55:2127–2140
- Raitsos DE, Beaugrand G, Georgopoulos D, Zenetos A, Paccucci-Papadopoulou AM, Theocharis A, Papathanassiou E (2010) Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. *Limnol Oceanogr* 55:1478–1484
- Reid PC, Beaugrand G (2012) Global synchrony of an accelerating rise in sea surface temperature. *J Mar Biol Assoc UK* 92:1435–1450
- Reid PC, Borges M, Svenden E (2001) A regime shift in the North Sea circa 1988 linked to changes in the north Sea horse mackerel fishery. *Fish Res* 50:163–171
- Reid PC, Colebrook JM, Matthews JBL, Aiken J, Continuous Plankton Recorder Team 1 (2003) The continuous plankton recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–173
- Reygondeau G, Beaugrand G (2011) Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Glob Change Biol* 17:756–766
- Rodionov SN (2004) A sequential algorithm for testing climate regime shift. *Geophys Res Lett* 31:L09204
- Rombouts I, Beaugrand G, Ibañez F, Gasparini S, Chiba S, Legendre L (2010) A multivariate approach to large-scale variation in marine planktonic copepod diversity and its environmental correlates. *Limnol Oceanogr* 55:2219–2229
- Rudnick DL, Davis RE (2003) Red noise and regime shifts. *Deep-Sea Res I* 50:691–699
- Rutherford S, D'Hondt S, Prell W (1999) Environmental controls on the geographic distribution of zooplankton diversity. *Nature* 400:749–753
- Sarmiento JL, Gruber N (2006) *Ocean biogeochemical dynamics*. Princeton University Press, Princeton, NJ, and Oxford
- Scheffer M (2009) *Critical transitions in nature and society*. Princeton University Press, Princeton, NJ
- Scheffer M, van Nes EH (2004) Mechanisms for marine regime shifts: Can we use lakes as microcosms for oceans? *Prog Oceanogr* 60:303–319
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman, New York, NY
- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *J Cons Int Explor Mer* 18:287–295
- Wanless S, Wright PJ, Harris MP, Elston DA (2004) Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a north sea aggregation over a 30-yr period. *Mar Ecol Prog Ser* 279:237–246
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8
- Warner AJ, Hays GC (1994) Sampling by the continuous plankton recorder survey. *Prog Oceanogr* 34:237–256
- Webster R (1973) Automatic soil-boundary location from transect data. *J Int Assoc Math Geol* 5:27–37
- Weijerman M, Lindeboom H, Zuur AF (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar Ecol Prog Ser* 298:21–39
- Woodruff S, Slutz R, Jenne R, Steurer P (1987) A comprehensive ocean-atmosphere dataset. *Bull Am Meteorol Soc* 68:1239–1250
- Yasunaka S, Hanawa K (2002) Regime shifts found in the northern hemisphere SST field. *J Meteorol Soc Jpn* 80:119–135

**Appendix 1.** List of species considered in the present study and the values of the first 2 eigenvectors after applying a PCA on each taxonomic group. Values above 0.5 are indicated in **bold** and correspond to a contribution of at least 25 % of the variable to the corresponding axis

Species or taxon	Values of the first normalised eigenvector	Values of the second normalised eigenvector	Species or taxon	Values of the first normalised eigenvector	Values of the second normalised eigenvector
<b>Diatoms</b>			<i>Ceratium horridum</i>	<b>0.6016</b>	0.059
<i>Asterionella glacialis</i>	<b>0.7735</b>	0.0186	<i>Ceratium lineatum</i>	<b>0.8008</b>	0.014
<i>Bacillaria paxillifer</i>	<b>0.57</b>	0.0871	<i>Ceratium longipes</i>	<b>0.5937</b>	<b>-0.5037</b>
<i>Bellerochea malleus</i>	<b>0.6358</b>	0.3865	<i>Ceratium macroceros</i>	0.4453	<b>-0.6484</b>
<i>Chaetoceros (Hyalochaete) spp.</i>	<b>0.552</b>	<b>-0.6643</b>	<i>Ceratium tripos</i>	<b>0.9116</b>	-0.0072
<i>Chaetoceros (Phaeoceros) spp.</i>	<b>0.5492</b>	<b>-0.5795</b>	<i>Dinophysis spp.</i>	0.4811	<b>0.6147</b>
<i>Coscinodiscus concinnus</i>	<b>0.535</b>	-0.0304	<i>Gonyaulax spp.</i>	-0.2034	<b>0.844</b>
<i>Cylindrotheca closterium</i>	<b>0.7363</b>	-0.0593	<i>Prorocentrum spp.</i>	-0.3496	<b>0.8255</b>
<i>Ditylum brightwellii</i>	<b>0.6122</b>	0.2565	<i>Protoperdinium spp.</i>	<b>0.6755</b>	<b>0.5499</b>
<i>Eucampia zodiacus</i>	0.29	0.0922	<b>Copepods</b>		
<i>Fragilaria spp.</i>	<b>0.5842</b>	-0.0589	<i>Acartia spp.</i>	-0.1714	<b>-0.5953</b>
<i>Rhizosolenia stolterfothii</i>	<b>0.7329</b>	0.3005	<i>Calanus finmarchicus</i>	<b>-0.8026</b>	-0.0013
<i>Gyrosigma spp.</i>	-0.0925	<b>0.5192</b>	<i>Calanus helgolandicus</i>	<b>0.8526</b>	-0.01
<i>Lauderia borealis</i>	<b>0.5393</b>	0.1722	<i>Candacia armata</i>	<b>0.772</b>	-0.1717
<i>Dactyliosolen mediterraneus</i>	0.4347	-0.2454	<i>Centropages hamatus</i>	-0.1826	<b>-0.6232</b>
<i>Navicula spp.</i>	0.1984	-0.4149	<i>Centropages typicus</i>	<b>0.7273</b>	-0.2344
<i>Odontella aurita</i>	<b>0.5861</b>	0.0906	<i>Labidocera wollastoni</i>	0.0027	-0.2214
<i>Odontella granulata</i>	-0.0086	0.1669	<i>Metridia lucens</i>	0.3029	-0.4941
<i>Odontella regia</i>	0.3874	<b>-0.6206</b>	<i>Para-pseudocalanus spp.</i>	-0.316	<b>-0.8551</b>
<i>Odontella rhombus</i>	0.3695	-0.2279	<i>Pseudocalanus elongatus (adult)</i>	-0.2548	<b>-0.7654</b>
<i>Odontella sinensis</i>	<b>0.6061</b>	0.4294	<i>Temora longicornis</i>	0.2802	<b>-0.6513</b>
<i>Paralia sulcata</i>	<b>0.8358</b>	0.2012	Harpacticoida (total)	0.2533	<b>-0.6242</b>
<i>Rhizosolenia alata alata</i>	<b>0.5037</b>	-0.4385	<i>Corycaeus spp.</i>	<b>0.7257</b>	-0.3987
<i>Rhizosolenia alata inermis</i>	0.1333	0.2456	<i>Oithona spp.</i>	<b>-0.6554</b>	<b>-0.6251</b>
<i>Nitzschia delicatissima</i>	<b>0.7237</b>	-0.0113	<b>Other holozooplankton</b>		
<i>Nitzschia seriata</i>	<b>0.8411</b>	0.1647	Gammaridea	<b>-0.8524</b>	0.0471
<i>Rhaphoneis amphiceros</i>	0.3046	<b>0.8305</b>	Hyperidea	<b>-0.609</b>	0.1563
<i>Rhizosolenia hebetata semispina</i>	0.1814	-0.4746	Cumacea	-0.0776	<b>0.6308</b>
<i>Rhizosolenia imbricata shrubsolei</i>	<b>0.8035</b>	0.2452	Mysidacea	-0.1598	<b>0.5216</b>
<i>Rhizosolenia styliformis</i>	0.2927	-0.2721	Euphausiacea (total)	0.2307	<b>-0.7495</b>
<i>Skeletonema costatum</i>	0.4975	-0.4099	Chaetognatha (eyecount)	<b>-0.7435</b>	0.0086
<i>Thalassionema nitzschioides</i>	<b>0.7264</b>	-0.0457	<i>Limacina retroversa</i>	<b>-0.7933</b>	-0.2489
<i>Thalassiosira spp.</i>	<b>0.4113</b>	0.126	<i>Clione limacina</i>	<b>-0.7895</b>	-0.3077
<i>Thalassiothrix longissima</i>	0.095	0.1382	Larvacea	0.0087	<b>0.7433</b>
<b>Dinoflagellates</b>			<b>Meroplankton</b>		
<i>Ceratium furca</i>	<b>0.8766</b>	0.2398	Decapoda larvae	<b>0.7892</b>	-0.2439
<i>Ceratium fusus</i>	<b>0.8587</b>	0.1522	Cyphonautes larvae	0.4741	<b>0.6827</b>
			Lamellibranchia larvae	0.1068	<b>0.8828</b>
			Echinoderm larvae	<b>0.7918</b>	-0.1816
			Fish eggs	0.4653	<b>-0.5725</b>
			Fish larvae	<b>0.7438</b>	0.2482