Volume 129 January 2014 ISSN 0924-7963

ELSEVIER

JOURNAL OF
MARINE
SYSTEMS

Journal of Marine Systems 129 (2014) 189–202

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Synchronous response of marine plankton ecosystems to climate in the Northeast Atlantic and the North Sea

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ARTICLE INFO

Article history:
Received 12 September 2012
Received in revised form 18 March 2013
Accepted 23 May 2013
Available online 28 May 2013

Keywords:
Climate change
North Atlantic
Long-term changes
Large-scale hydro-climatic indices
Phytoplankton
Zooplankton

ABSTRACT

Over the last few decades, global warming has accelerated both the rate and magnitude of changes observed in many functional units of the Earth System. In this context, plankton are sentinel organisms because they are sensitive to subtle levels of changes in temperature and might help in identifying the current effects of climate change on pelagic ecosystems. In this paper, we performed a comparative approach in two regions of the North Atlantic (i.e. the Northeast Atlantic and the North Sea) to explore the relationships between changes in marine plankton, the regional physico-chemical environment and large-scale hydro-climatic forcing using four key indices: the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), the East Atlantic (EA) pattern and Northern Hemisphere Temperature (NHT) anomalies. Our analyses suggest that long-term changes in the states of the two ecosystems were synchronous and correlated to the same large-scale hydro-climatic variables: NHT anomalies, the AMO and to a lesser extent the EA pattern. No significant correlation was found between long-term ecosystem modifications and the state of the NAO. Our results suggest that the effect of climate on these ecosystems has mainly occurred in both regions through the modulation of the thermal regime.

1. Introduction

Natural climatic variability occurs over a multitude of temporal scales, ranging from diurnal cycles to multi-millennial patterns (Ghil, 2003) and influences many natural systems of the planet (Drinkwater et al., 2003). In addition to the effect of climatic variability, global warming has become unambiguous, and the worldwide increase in temperatures has clearly accelerated the rate of changes observed in virtually all compartments of the Earth System (IPCC, 2007).

Climate change may directly influence the performance of individuals through an alteration of the physiology, the morphology and the behaviour (Harley et al., 2006). At the community level, climate influences species recruitment through changes in population dynamics and dispersal. At the ecosystem scale, trophic cascade intensifies the effect of climate change from phytoplankton and zooplankton to higher trophic levels, altering the strength and direction of species interaction (Kirby and Beaugrand, 2009; Richardson and Schoeman, 2004). The combination of these effects results in emergent ecological responses, which include both phenological and biogeographical shifts (Beaugrand et al., 2002; Edwards, 2004; Parmesan, 2006; Perry et al., 2005). In this context, the influence of climate-induced forcing on plankton has been particularly studied, this group being sensitive to subtle changes in temperature (Helaouët and Beaugrand, 2007; Taylor et al., 2002).

Much attention has also been given to two of the dominant large-scale patterns of climatic variability of the North Atlantic such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) which can attenuate or exacerbate the effects of global warming at regional scales. Since large-scale indices integrate the overall physical variability of the system, they refer to the long-term averaged distributions of near-surface hydro-climatic elements (Stenseth et al., 2002). These large-scale climatic sources of variability on regional hydro-climatic processes produce coherent variations over large regions on long time scales and play an important role on the distribution of some plankton species (Hurrell and Deser, 2009; Stenseth et al., 2002). For example, diatoms are sensitive to the level of mixing of the water column (Beaugrand, 2009; Margalef, 1978) and copepods are influenced by the level of turbulence which modulates the contact rate between prey and predator (Rothschild and Osborn, 1988). Precipitation, by its effect on thermohaline stratification (Falkowski et al., 1998) and the volume of river runoff (Harley et al., 2006), modulates both vertical and horizontal nutrient inputs, which in turn may have subsequent effects on primary production (Goberville et al., 2011; Lotze and Worm, 2002). Both wind intensity and direction, by their forcing on mixing processes and oceanic currents, may also influence nutrient availability at the surface (Hinder et al., 2012; Longhurst, 2007). The list, far from being exhaustive, shows the multitude of influences through which climatic variability can affect pelagic ecosystems (Kirby and Beaugrand, 2009).

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http://dx.doi.org/10.1016/j.jmarsys.2013.05.008

Temperature is a cardinal factor governing long-term changes in both biological and ecological systems. Beaugrand et al. (2008) showed that temperature was important in determining the dynamic regime of both the North Atlantic and North Sea systems. Many studies have provided evidence that temperature influences physico-chemical, physiological and biological processes, from the cell to the biosphere level (e.g. Beaugrand, 2009; Brown et al., 2004; Sarmiento et al., 2004). Temperature not only directly influences an organism's metabolism or interplay among species (Kirby and Beaugrand, 2009) but also controls other equally important environmental parameters (Harley et al., 2006). For example, temperature has an influence on water stratification, modulating nutrient cycling, photosynthetic rate (Shaw et al., 2003) and primary production (Behrenfeld, 2010; Sarmiento and Gruber, 2006). At a global scale, temperature patterns govern the location of major provinces and biomes (Longhurst, 2007; Reygondeau and Beaugrand, 2011a; Sarmiento et al., 2004).

In this paper, we examined long-term annual changes in the abundance of three marine plankton groups (i.e. dinoflagellates, diatoms and copepods) in relation to both regional and large-scale hydro-climatic forcing. First, we investigated as to what extent large-scale hydro-climatic variability influences regional climate. Second, we applied a comparative approach, analysing the long-term changes of two ecosystems (the Northeast Atlantic and the North Sea) in relation to hydro-climatic forcing. Our results suggest that a common hydro-climatic forcing has influenced these two regions and that the processes by which climate might propagate through ecosystems are mainly influenced by temperature.

2. Materials and methods

2.1. Areas of study

First, we estimated the potential spatial variation of large-scale hydro-climatic forcing at the scale of the North Atlantic (105°W–45°E and 0°N–85°N).

Secondly, two regions were selected to examine the relationships between long-term changes in the abundance of diatoms, dinoflagellates and copepods and both regional and large-scale hydro-climatic variability: the North Sea (4°W–10°E and 51.5°N–60°N) and the Northeast Atlantic (25°W–5°W and 47°N–60°N; Fig. 1).

2.2. Hydro-climatic parameters

2.2.1. Large-scale hydro-climatic indices

Four large-scale hydro-climatic indices were selected to examine their potential influence on the long-term changes in the abundance of the three taxonomic groups in the two studied areas.

The Atlantic Multidecadal Oscillation (AMO) is an index of multidecadal ocean/atmosphere natural variability in the range of 0.4 °C in many oceanic regions and a periodicity of about 60–80 years (Enfield et al., 2001). Although the internal variability in the Atlantic meridional overturning circulation is the determining factor for the AMO (Ottera et al., 2010), recent studies established that changes in volcanic and aerosols forcing also exert a significant role (Booth et al., 2012). Many studies provided compelling evidence that this oceanic oscillation might have been responsible for substantial changes in the regional climate and especially for anomalies in precipitation and surface temperature (e.g. over Western Europe, the United States, and Southern Mexico; Edwards et al., 2013; Enfield et al., 2001; Keenlyside et al., 2008; Sutton and Hodson, 2005). We used the index constructed from Extended Reconstruction SST (ERSST) data and averaged in the area of 25 to 60°N and 7 to 75°W, minus regression on global mean temperature (National Oceanic & Atmospheric Administration: NOAA; http://www.esrl.noaa.gov/psd/data/timeseries/AMO/).

The winter North Atlantic Oscillation (NAO; Hurrell, 1995a) describes the basin-scale gradient of atmospheric pressures over the North Atlantic between the high pressures centred on the subtropical Atlantic and the low pressures over Iceland (Dickson and Turrell, 2000). This oscillation has been correlated with a large range of physical and biological indicators, e.g. the paths of Atlantic storms and

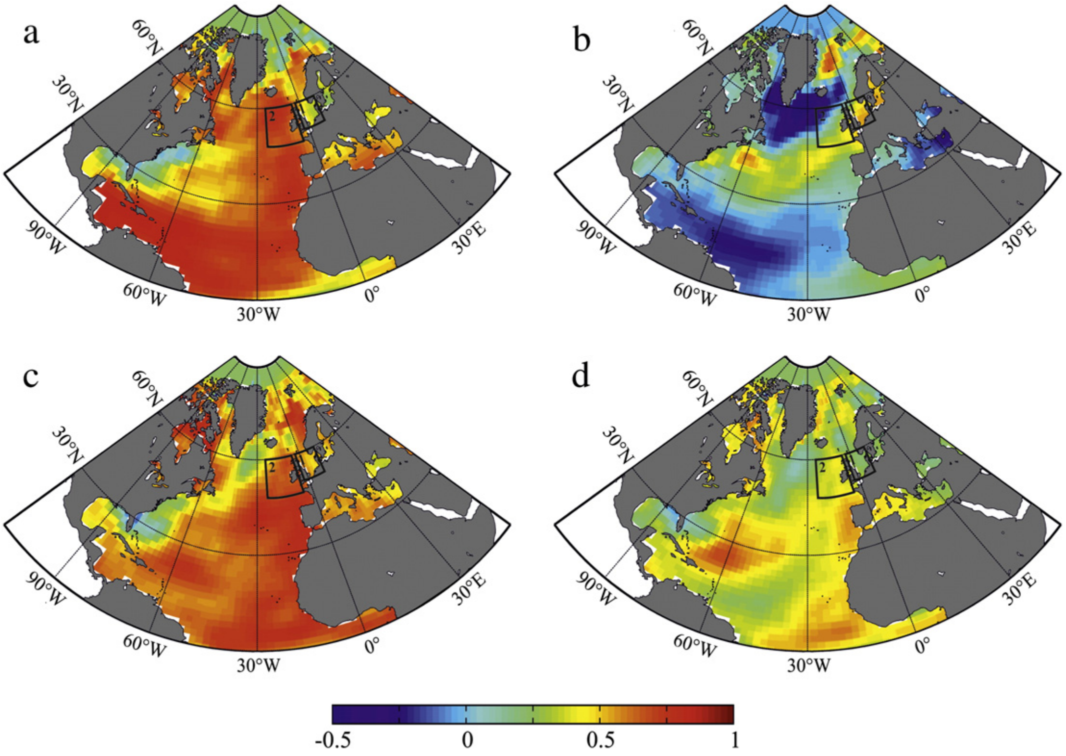

Fig. 1. Correlation maps between some large-scale hydro-climatic indices and annual sea surface temperature in the North Atlantic Ocean. (a) The Atlantic Multidecadal Oscillation (AMO) index. (b) The winter North Atlantic Oscillation (NAO). (c) Northern Hemisphere Temperature anomalies (NHT anomalies). (d) The East Atlantic (EA) pattern. The two studied regions are mentioned: (1) the North Sea (4°W–10°E and 51.5°N–60°N) and (2) the Northeast Atlantic (25°W–5°W and 47°N–60°N).

their intensity (Hurrell, 1995b), precipitation patterns (Hurrell, 1995a), or fluctuations in the species productivity (e.g. Alheit and Hagen, 1997). The winter NAO index used in this study is based on a principal component analysis performed on sea level pressures over the North Atlantic sector for months from December to March (Hurrell et al., 2001). This index was downloaded from http://climatedataguide.ucar.edu/category/data-set-variables/climate-indices.

The East Atlantic (EA) pattern, structurally similar to the NAO, is the second of three prominent modes of low-frequency variability over the North Atlantic (Msadek and Frankignoul, 2009). The EA pattern is defined by a centre of action over 55°N and 20°–35°W (Barnston and Livezey, 1987). This pattern has a strong influence on the environment in Western Europe (Msadek and Frankignoul, 2009). Data were provided by the National Oceanic & Atmospheric Administration (NOAA; http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml).

Northern Hemisphere Temperature (NHT) anomalies, provided by the Hadley Centre for Climate Prediction and Research, were utilised as a proxy of the potential effect of global warming in the Northern Hemisphere, although this index also integrates hydro-climatic variability (Beaugrand and Reid, 2003).

2.2.2. Regional climatic variables

The influence of Sea Surface Temperatures (SSTs) on plankton was assessed using the dataset ERSST_V3. The dataset is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have been applied to produce a stable monthly reconstruction, on a 1° × 1° spatial grid (Smith et al., 2008).

To evaluate the impact of regional climate on plankton species, annually gridded data on sea level pressure (SLP), wind intensity and both zonal (i.e. west to east component of the wind) and meridional (i.e. the south to north component of the wind) components were used. Directional wind time series were obtained from averaging four times per day data (Kalnay et al., 1996). Wind intensity being considered as a surface pressure gradient (Henderson-Sellers and Robinson, 1986), the average direction and strength of the wind can be calculated from the Pythagorean formula combining the information on both zonal and meridional winds (Goberville et al., 2010). Precipitation data were also used, as this parameter influences both the inputs of freshwater and nutrients from land to ocean. The effect of solar radiation on phytoplanktonic abundance was assessed by using downward solar radiation flux data (Raitsos et al., 2006).

The winds, precipitation and downward solar radiation data were obtained from the National Centers for Environmental Prediction (NCEP) and the National Center for Atmospheric Research (NCAR). Both the methodology of the NCEP–NCAR reanalysis and the numerical procedures applied on data were discussed in detail in Kalnay et al. (1996) and Kistler et al. (2000). Gridded climatic data were analysed between 1958 and 2007.

2.2.3. Environmental parameters

Environmental parameters consisted of surface (top 10 m of water column) nutrient concentrations (nitrates, phosphates and silicates), oxygen, salinity and chlorophyll *a*. These data were provided by both the International Council for the Exploration of the Sea (ICES; http://www.ices.dk/ocean/) and the World Ocean Database (WOD; http://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html). For each variable (i.e. nitrate, phosphate and silicate concentration, oxygen, salinity and chlorophyll *a*), we first estimated time series at a monthly scale over each selected area (i.e. the North Sea and the Northeast Atlantic). Annual time series were then calculated by averaging the monthly values for the period 1958–2007 in both study areas.

2.3. Biological data

Biological data used in this study were collected by the Continuous Plankton Recorder (CPR) survey. This large-scale plankton monitoring programme has operated on a routine monthly basis in the North Atlantic and in the North Sea since 1946 (Reid et al., 2003a; Warner and Hays, 1994). Sampling is carried out at a constant depth (approximately 6 to 7 m) of the water column. More details on methods and contents of this dataset are described in Reid et al. (2003a) and Batten et al. (2003).

Changes in the annual abundance of all species or taxonomic groups sampled by the CPR survey were investigated. An annual mean was calculated for all species or taxonomic groups using a procedure similar to the method CIMOTS ('Copepod Indicator Monitoring Toolbox System') described in Beaugrand (2004). Then, species or taxonomic groups with an annual relative abundance >0.001 and a presence >30% for all years of the period 1958–2007 were selected using the procedure applied in Ibanez and Dauvin (1998). This procedure allowed the selection of 68 species or taxonomic groups in the Northeast Atlantic (14 diatom species, 13 dinoflagellate species, and 41 copepod species) and 53 species or taxonomic groups in the North Sea (17 diatom species, 12 dinoflagellate species, and 24 copepod species). Abundance data were transformed using the function $\log_{10}(x + 1)$.

2.4. Analysis 1: Correlation maps between large-scale hydro-climatic indices and annual SSTs

We calculated the correlations between large-scale hydro-climatic indices and annual SSTs for each geographical cell of a grid 1° longitude × 1° latitude corresponding to the Northern Hemisphere for the period 1958 to 2007 (Fig. 1). We considered four indices: the AMO index, the winter NAO index, the EA pattern and the NHT anomalies.

2.5. Analysis 2: Long-term fluctuations in plankton in relation to environmental and regional climatic changes

Both the spatial and temporal sampling heterogeneities of the two studied areas may bias our time series (Hays et al., 1993). Sampling heterogeneity decreases the signal-to-noise ratio at the year-to-year scale. To reduce this effect, we applied a simple moving average on each time series: order-1 for the North Sea dataset and order-2 for the Northeast Atlantic dataset, order-2 being explained by a higher sampling heterogeneity in the Northeast Atlantic than in the North Sea. This method highlights long-term variability and minimises short-term fluctuations by reducing the noise inherent to these data (Legendre and Legendre, 1998).

To extract the major long-term changes that took place in the environment, the regional climate and the different plankton groups (diatoms, dinoflagellates, and copepods) in both study areas, standardised principal component analyses (PCAs for tables with missing data; Bouvier, 1977) were performed separately on correlation matrices during the period 1958–2007 for each annual dataset: (1) environmental variables (i.e. nitrate, phosphate and silicate concentration, oxygen, salinity and chlorophyll *a*), (2) regional climatic variables (i.e. SSTs, SLP, wind intensity and direction, mean precipitation and downward solar radiation flux data), (3) diatoms, (4) dinoflagellates and (5) copepods (Fig. S1). This statistical technique gave a summary of the dominant information by revealing the largest amount of total variance within each dataset for each selected area (i.e. the North Sea and the Northeast Atlantic). Therefore a total of ten PCAs were performed and we retained the first two principal components (PCs) for further examination (Figs. 2 & 3). To examine how moving averages influenced our PCAs, we compared the principal components from the original matrices and matrices in which the moving averages were applied (Fig. S2).

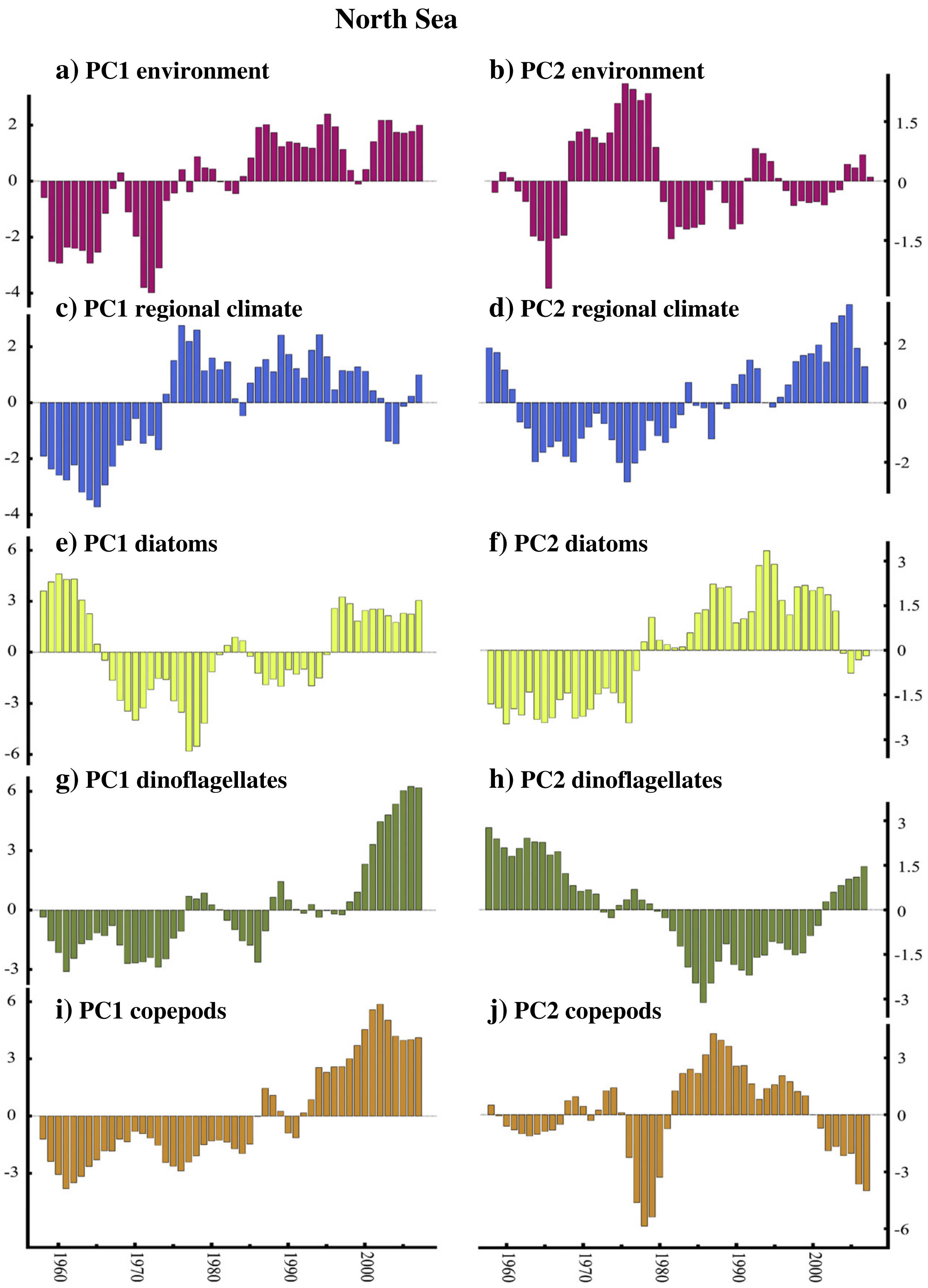

Fig. 2. Long-term changes in the North Sea (1958–2007). (a) First and (b) second principal component (PC) calculated from a standardised PCA performed on environmental parameters; (c) first and (d) second PC calculated from a standardised PCA applied on regional climate; (e) first and (f) second PC calculated from a standardised PCA calculated on diatoms; (g) first and (h) second PC computed from a standardised PCA on dinoflagellates; and (i) first and (j) second PC obtained from a standardised PCA on copepods.

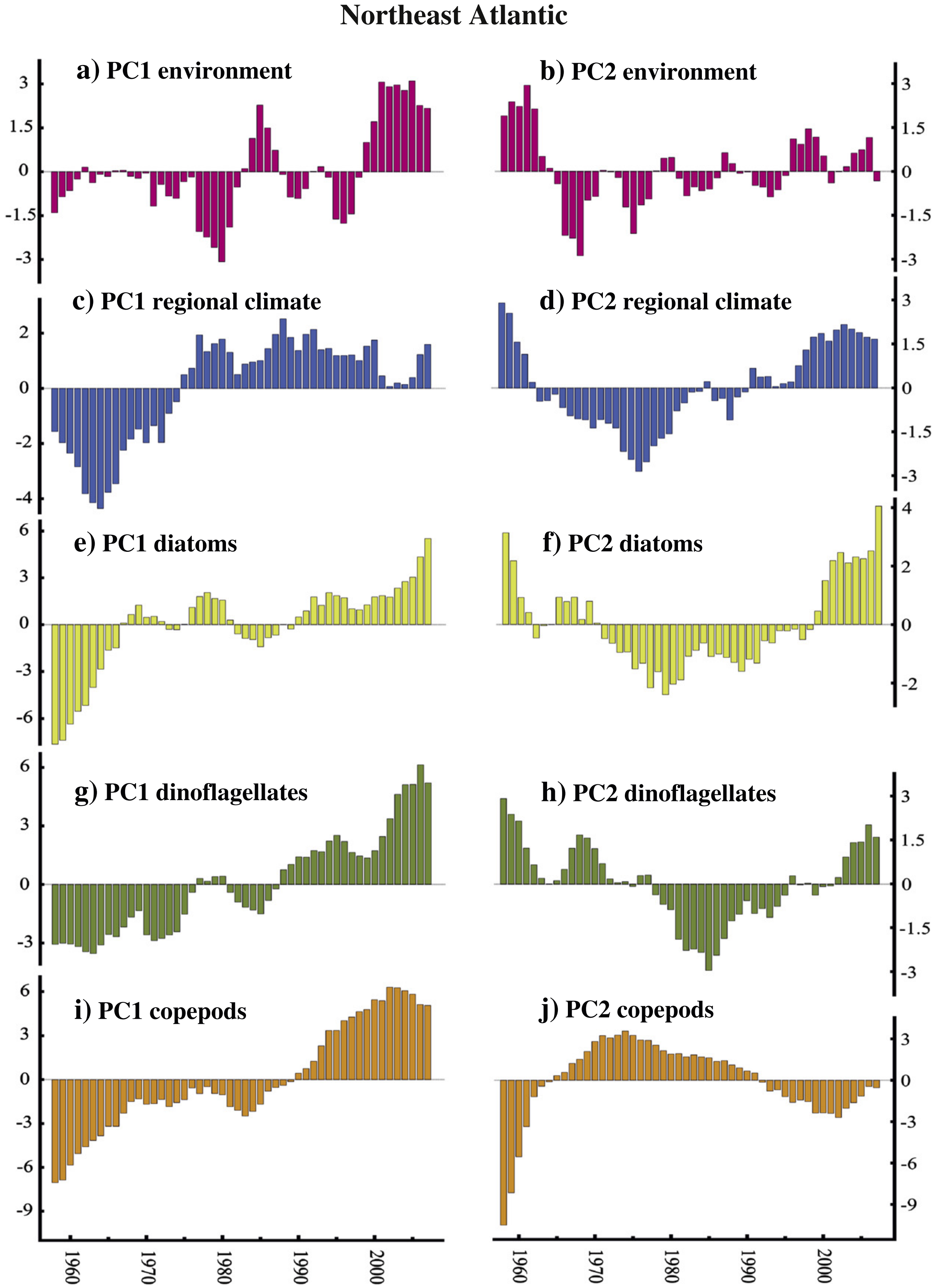

Fig. 3. Long-term changes in the Northeast Atlantic (1958–2007). (a) First and (b) second principal component (PC) calculated from a standardised PCA performed on environmental parameters; (c) first and (d) second PC calculated from a standardised PCA applied on regional climate; (e) first and (f) second PC calculated from a standardised PCA calculated on diatoms; (g) first and (h) second PC computed from a standardised PCA on dinoflagellates; and (i) first and (j) second PC obtained from a standardised PCA on copepods.

2.6. Analysis 3: Relationships among PCs and selection

For each region, results from previous PCAs were then combined into a single matrix for identifying the most significant components involved in changes (Fig. S1). The matrix 50 years × 10 variables had the following variables: PC1 and PC2 environmental parameters, PC1 and PC2 regional climate, PC1 and PC2 diatom abundance, PC1 and PC2 dinoflagellate abundance, and PC1 and PC2 copepod abundance. We calculated correlation matrix C and then converted this table into a distance matrix D by applying the following transformation:

$$D = 1-|C|. \tag{1}$$

The hierarchical flexible agglomerative clustering method (Lance and Williams, 1967) was then applied on the distance matrix 10 × 10 PCs to determine relationships between variables. This general model encompasses most of the agglomerative clustering model (Lance and Williams, 1967). Here, α_j was fixed to 0.625, α_m to 0.625, β to -0.25 and γ to 0 so that the method was close to the unweighted centroid clustering (or unweighted pair-group centroid method, Legendre and Legendre, 1998). For each region, this analysis allowed us to select only the PCs that had a distance <0.5 on the dendrogram (Fig. 4). The PCs were then standardised between −1 and 1 and represented by a contour diagram (Fig. 5), their trends being ordered to highlight both common patterns of variability and abrupt shifts over the period 1958–2007. Using the results from the cluster analysis, we grouped together PCs into a single matrix for each region. To represent the North Sea, we selected 9 variables: PC1 and PC2 environmental parameters, PC1 and PC2 regional climate, PC1 and PC2 diatoms, PC1 and PC2 dinoflagellates and PC1 copepods. For the Northeast Atlantic, we retained 7 variables: PC1 and PC2 regional climate, PC1 and PC2 diatoms, PC1 dinoflagellates, and PC1 and PC2 copepods. To summarise the main long-term changes in each region, we then applied two standardised PCAs on the resulting tables (Fig. S1). This procedure was applied to reduce the number of correlation analyses and their implications in terms of multiple testing (Legendre and Legendre, 1998).

2.7. Analysis 4: Influence of large-scale hydro-climatic forcing

The Pearson linear correlation coefficient was used to assess the relationships between the first two PCs and large-scale hydro-climatic forcing in the North Sea and the Northeast Atlantic (Table 1 and Fig. 5). Probabilities were estimated and corrected to account for temporal autocorrelation. Box and Jenkins' (1976) autocorrelation function modified by Chatfield (1996) was calculated. The autocorrelation function was then applied to adjust the degree of freedom using Chelton's (1984) formula as applied by Pyper and Peterman (1998), this type of correction giving better results than the Garrett and Petrie (1981) method.

Relationships between each large-scale hydro-climatic index and the first two PCs from the two PCAs were then investigated in the North Sea and the Northeast Atlantic. Fig. 7 combines year-to-year changes in each study area and large-scale hydro-climatic indices in a single graph (called biplot; Gabriel, 1971) so that their association can be analysed graphically. The first two PCs were represented in a plane and displayed similarities among years. For each year of the period 1958–2007, the value of each large-scale hydro-climatic variable was then assigned. The values of hydro-climatic variables were interpolated and represented by a colour scale, blue gradient corresponding to a negative phase of the index and red to a positive phase. This representation showed the time series of responses of each area and relationships with the descriptor (i.e. each large-scale index) and allowed to characterise each year by reference to changes in large-scale hydro-climatic indices.

3. Results

3.1. Correlation maps between large-scale hydro-climatic indices and annual SSTs

The spatial pattern of correlation between the AMO index and annual SSTs exhibited high positive values in the western part of the tropical North Atlantic and in the Northeast Atlantic (Fig. 1a). No correlation was found in the North Sea. A classical tri-polar pattern between the winter NAO index and annual SSTs was identified, with negative correlations over the subpolar and subtropical regions and positive

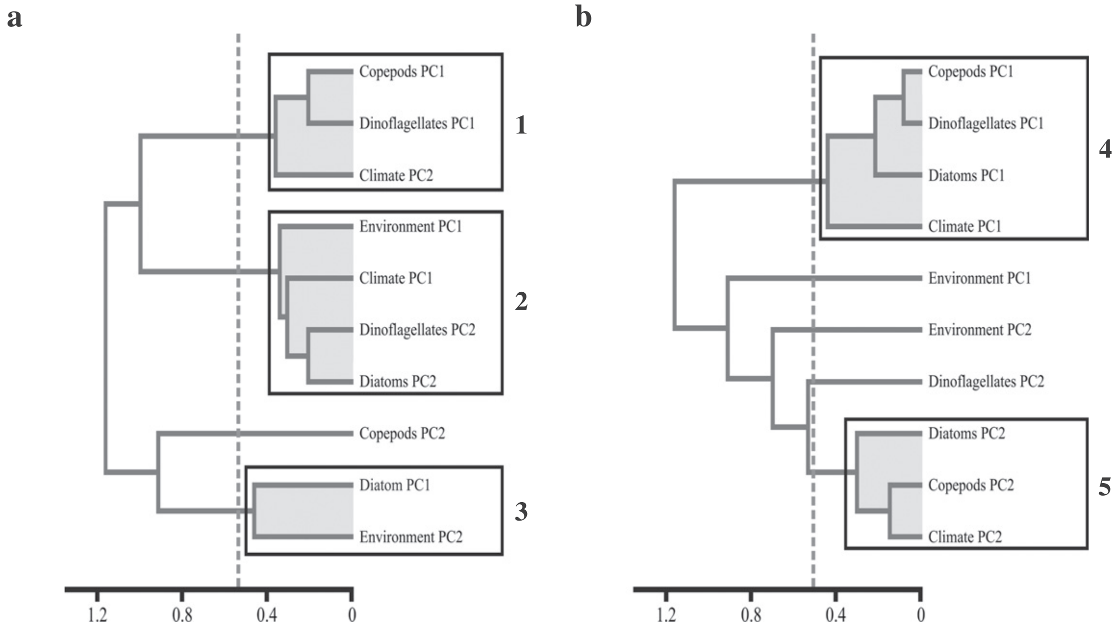

Fig. 4. Dendrograms showing the results of the cluster analyses performed on the distance matrix 10 × 10 variables to identify relationships among variables (a) in the North Sea and (b) in the Northeast Atlantic for the period 1958–2007 (see Analysis 3, Fig. S1). For each region, we chose only the variables (PCs) that had a distance <0.5 on the dendrograms. Numbers in bold represent the number of the group (see Results 3.3).

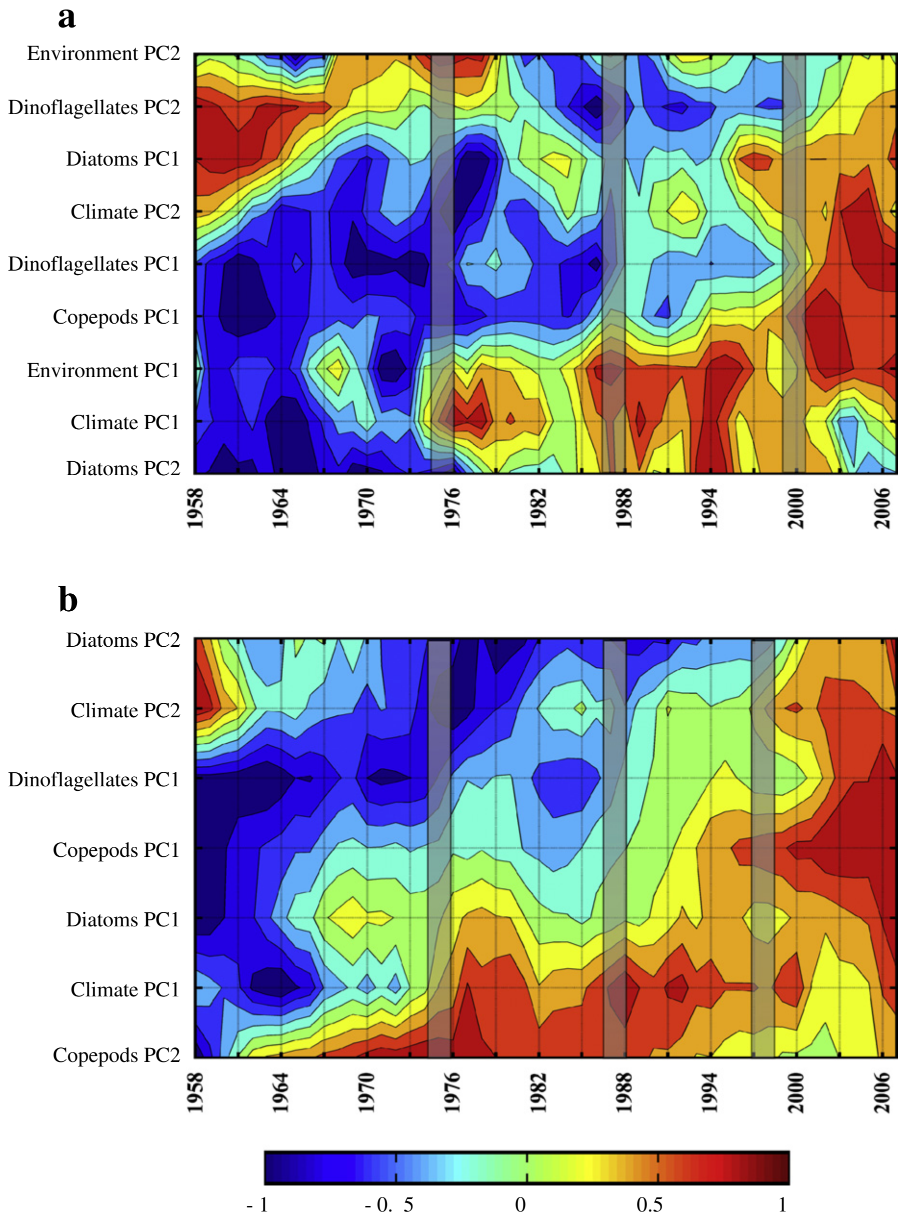

Fig. 5. Long-term changes (1958–2007) in the first two principal components that were calculated from a standardised PCA on environmental parameters, regional climate and plankton (dinoflagellates, diatoms, and copepods): (a) in the North Sea and (b) in the Northeast Atlantic. Only variables selected from the cluster analyses were used (see Analysis 3, Fig. S1 and Fig. 4). The contour diagrams were normalised between −1 and 1. The grey bars show the four periods (see Results 3.3).

Table 1
Pearson linear correlations between the four large-scale hydro-climatic indices and the first two principal components (PCs) calculated by standardised PCA performed for each region on the variables selected from the dendrogram (see Analysis 4, Fig. S1, Fig. 4). Probabilities were corrected to account for temporal autocorrelation with the method recommended by Pyper and Peterman (1998). Correlations $r > 0.5$ are in bold.

		Principal component			
		1		2	
		r	p	r	p
North Sea	AMO	0.401	0.431	**0.780**	**0.023**
	NHT	**0.814**	**0.187**	0.488	0.266
	NAO	**0.533**	**0.050**	0.078	0.799
	EA pattern	**0.811**	**0.096**	0.323	0.435
Northeast Atlantic	AMO	0.486	0.328	**0.769**	**0.026**
	NHT	**0.884**	**0.116**	0.379	0.459
	NAO	**0.538**	**0.135**	−0.126	0.729
	EA pattern	**0.791**	**0.111**	0.297	0.518

correlations in the mid-latitudes of the North Atlantic (Fig. 1b). The spatial pattern of correlations between NHT anomalies and annual SSTs was positive everywhere except along the path of the Gulf Stream and the Oceanic Polar Front (Dietrich, 1964) supporting that interannual surface temperature changes could be primarily related to ocean circulation changes in these regions (Zhang, 2008). Its correlation was also strong in the Northeast Atlantic, including the North Sea (Fig. 1c). The correlations of the EA pattern with the annual SSTs were particularly highly positive in both tropical and subtropical regions and in the Northeast Atlantic, excluding the North Sea and the Subarctic Gyre and the oceanic regions crossed by the Gulf Stream (Fig. 1d).

3.2. Long-term changes in the North Sea and Northeast Atlantic ecosystem states

For each region, a total of five PCAs were performed on the following datasets: (1) environmental variables (i.e. nitrate, phosphate and silicate concentration, oxygen, salinity and chlorophyll *a*), (2) regional climatic variables (i.e. SSTs, SLP, wind intensity and direction, mean precipitation and downward solar radiation flux data), (3) diatoms, (4) dinoflagellates and (5) copepods.

3.2.1. The North Sea (Fig. 2)

The higher frequency variability in the first PC of the PCA on environmental variables (55.41% of the total variability) exhibited a pronounced increase during the 1980s (Fig. 2a). Nutrients, chlorophyll *a* (positively) and salinity (negatively) mainly contributed to the changes (Table S1). The increase in the component corresponded to both an increase in nutrient concentrations and chlorophyll *a* and a decline in salinity. The examination of the second PC (22.08% of the total variability) showed variability with time scales of between 7 and 12 years (Fig. 2b). Positive values were observed during the 1970s. The largest contributions to these changes were from oxygen and salinity (Table S1).

Long-term changes in PC1 of the PCA performed on regional climate (46.23% of the total variability) showed low values of the component from 1958 to 1973, followed by a period of high values until 2000 (Fig. 2c). Examination of the first eigenvector indicated that wind intensity, its zonal component and mean precipitation were positively related to the first PC whereas meridional winds were negatively correlated (Table S2). The increase exhibited by the component suggested an augmentation in atmospheric circulation and precipitation from 1975 to 1995 and concomitant lower meridional winds. Long-term changes in PC2 (30.51% of the total variability) exhibited high values from 1958 to 1962 and after 1996 (Fig. 2d). Sea-level pressure was negatively related to long-term changes in the second PC indicating a reduction in oceanic circulation whereas temperature was highly positively correlated revealing an increase in SSTs (Table S2).

The first principal component from the PCA performed on diatoms (PC1 = 43.65% of the total variability) exhibited a decrease from 1960 to 1977 followed by an increase in the trend with two periods of relative stability and positive high values from 1996 onwards (Fig. 2e). Diatoms such as *Asterionella glacialis* and *Paralia sulcata* were positively correlated to the component (Table S3), suggesting a rise in their abundance. The second PC (18.03% of the total variability) showed a pronounced increase from 1976 to the mid-1990s, followed by a decline until 2007 (Fig. 2f). Species such as *Chaetoceros* (*Phaeoceros*) spp. and *Rhizosolenia hebetata semispina* were negatively correlated to the component (Table S3).

Superimposed on variability with a time scale of 8–10 years, the examination of the long-term changes in PC1 of the PCA on dinoflagellates (55.89% of the total variability) exhibited an increase from 1998 onwards (Fig. 2g). The second PC (21.79% of the total variability) showed both a decrease from 1958 to 1986 and a marked increase from the mid-1980s until 2007 (Fig. 2h). The examination of the first two eigenvectors indicated a reduction in the abundance of almost all dinoflagellates such as all *Ceratium* species and *Scrippsiella* spp. (Table S4).

The first component of the PCA on copepods (30.64% of the total variability) showed an increase in the trend with pronounced positive values from 1985 onwards (Fig. 2i). Species such as *Calanus helgolandicus* and *Centropages typicus* were positively correlated to the component (Table S5), revealing an augmentation in their abundances. In contrast, species such as *Calanus finmarchicus* were negatively related to PC1, showing a decrease of its abundance (Table S5). After a decade (1978–1987) of rapid augmentation, year-to-year changes in PC2 (22.29% of the total variability) exhibited a continuous decline from 1987 (Fig. 2j). Species such as *Acartia* spp. and *Temora longicornis* were strongly positively correlated to the second component, indicating a decline in the abundance of these species (Table S5).

3.2.2. Northeast Atlantic (Fig. 3)

After a period of low year-to-year changes from 1958 to 1976, long-term changes in the first PC of the PCA on environmental variables (40.05% of the total variability) exhibited periods of high negative (1977–1982 and 1989–1998) and positive (1984–1987 and 1999–2007) anomalies (Fig. 3a). Nutrients (positively) and oxygen (negatively) mainly contributed to the changes (Table S1). The increase in the component after 1998 corresponded to an increase in nutrient concentrations and a decrease in oxygen. The second PC (25.14% of the total variability) showed variability at a time scale of about 5–6 years with high positive anomalies during the last decade (Fig. 3b). Chlorophyll *a* (positively) and salinity (negatively) were strongly correlated with the component, indicating an increase in primary production and a reduction in salinity in the water column during the period 1968–2007 (Table S1).

The first PC of the PCA performed on regional climate (52.51% of the total variability) displayed a shift between a period characterised by negative anomalies (1958–1974) and a period of positive anomalies (1975–2007) (Fig. 3c). Wind intensity, zonal wind and precipitation (positively), and SLP and solar radiation (negatively) were strongly related to the first PC (Table S2), showing stability in these regional climatic variables over the last 30 years. Year-to-year changes in the second PC (29.31% of the total variability) exhibited a strong decrease from 1958 to the mid-1970s followed by a pronounced increase until 2007 (Fig. 3d). SSTs predominantly contributed to the changes, revealing a clear increase in SSTs in the region since the mid-1970s and especially from 1997 (Table S2).

PC1 of the PCA performed on diatoms (52.86% of the total variability) expressed a continuous increase, which accelerated after the early 2000s (Fig. 3e). All species were negatively related to this component (Table S3). Year-to-year changes in the second PC (16.21% of the total variability) exhibited a decrease from 1958 to 1980 followed by a pronounced increase until 2007 (Fig. 3f). Species such as *Rhizosolenia alata inermis* were strongly negatively correlated to the component, revealing a reduction in their abundance since 1980, phenomenon exacerbated from 2000 onwards (Table S3).

Year-to-year changes in the first PC of the PCA on dinoflagellates (56.65% of the total variability) showed an increasing trend over the period, with the highest values since 2000 (Fig. 3g). The study of the first eigenvector exhibited a clear decrease in virtually all dinoflagellates such as *Ceratium furca* and *Ceratium fusus* (Table S4). Long-term changes in the second component (14.86% of the total variability) revealed an increasing trend since 1985 (Fig. 3h). Species such as *Prorocentrum* spp. were negatively related to the PC2, revealing a decrease in the dinoflagellate abundances from the mid-1980s onwards (Table S4).

The first component of the PCA on copepods (32.32% of the total variability) revealed an increasing trend with two phases of rapid increase: 1958–1978 and 1989–2002 (Fig. 3i). Species such as *C. finmarchicus* (negatively) and *C. helgolandicus* (positively) were strongly correlated to the first component (Table S5). *C. finmarchicus* declined in abundance from 1958 to 2007, while *C. helgolandicus* increased. The second component (19.28% of the total variability) exhibited an increase from 1958 to the mid-1970s, followed by a decrease until 2007 (Fig. 3j). Inspection of the eigenvectors showed that species such as *C. typicus* and *Sapphirina* spp. were mostly negatively correlated to the second component, suggesting an increase in the abundance of these species from 1975 (Table S5).

A graphical examination of the results from the sensitivity analysis showed that the principal components were not significantly affected by the application of simple moving averages (Fig. S2).

3.3. Identification of the relationships among variables

By calculating a cluster analysis performed on a matrix of association (Fig. 4), we only retained principal components that summarise the main information for each region. This procedure decreased the number of correlation analyses and the potential risk of a type I error (i.e. finding too many significant correlations).

Cluster analysis for the North Sea dataset distinguished 3 main groups (Clusters 1, 2 and 3) and identified that the more relevant variables were: PC1 and PC2 environmental variables, PC1 and PC2 regional climate, PC1 and PC2 diatoms, PC1 and PC2 dinoflagellates and PC1 copepods (Fig. 4a). Cluster 1 encompassed PC2 regional climate and the first PCs of the PCA on both dinoflagellate and copepod assemblages, revealing concomitant changes in regional SST, oceanic circulation and species such as *Ceratium* spp. and *C. finmarchicus*. Cluster 2 gathered together PC1 of the PCA performed on environmental parameters, PC1 of regional climate and PC2 of the PCA on diatoms and dinoflagellates. Long-term changes in atmospheric circulation, both nutrient and chlorophyll *a* concentrations and species such as *Chaetoceros* spp. and *Scrippsiella* spp. were thus associated. Cluster 3 grouped PC1 of the PCA on diatom species and PC2 environment together.

Cluster analysis performed on the Northeast Atlantic Sea dataset identified 2 main groups (Clusters 4 and 5) and the most pertinent indices were: regional climate (PC1 and PC2), diatoms (PC1 and PC2), dinoflagellates (PC1), and copepods (PC1 and PC2) (Fig. 4b). Cluster 4 included the PC1 of the PCAs performed on regional climate, diatom, dinoflagellate and copepod abundances. This result showed that changes in most components of regional climate (i.e. atmospheric and oceanic circulations, mean precipitation and solar radiation) were related to long-term changes in planktonic species such as *Nitzschia delicatissima* (for diatoms), *C. furca* (for dinoflagellates) and *C. finmarchicus* (for copepods). Cluster 5 included the second PCs of regional climate and both diatoms and copepods, indicating that year-to-year changes in SST were associated with changes in diatom species such as *R. alata inermis* and copepods such as *Sapphirina* spp.

To evaluate ecosystem changes and potential shifts in both study areas, the principal components calculated from the different PCAs (see Analysis 2) and selected by clustering (see Analysis 3) were represented in a same figure. Principal components were standardised between −1 and 1 and represented by a contour diagram (Fig. 5). Negative values (blue gradient) corresponded to negative values of principal components (i.e. PC1 copepods in the North Sea for the period 1958–mid-1980s). Positive values (yellow-to-red gradient) corresponded to positive values of principal components (i.e. PC1 copepods in the North Sea for the period 1992–2007). Not all PCs reacted at the same time and gradual modifications were observed over the period. In the North Sea (Fig. 5a) and the Northeast Atlantic (Fig. 5b), we identified four periods: (1) from 1958 until the mid-1970s with predominance of negative values (in blue), (2) from the mid-1970s until the late 1980s with attenuation of the most negative values and emergence of some positive values (in red, e.g. PC1s climate and environment in the North Sea; PC1s climate and diatoms in Northeast Atlantic); (3) from the late 1980s until the end of the 20th century with an intensification of positive values and few negative values; and (4) from 2000 onwards, with a prevalence of positive values for virtually all principal components.

3.4. Influence of large-scale hydro-climatic processes

We then performed two subsequent principal component analyses, the first on the table 50 years × 9 variables (see Fig. 5a; the North Sea) and the second on the table 50 years × 7 variables (see Fig. 5b; the Northeast Atlantic). For each region, linear correlations between the first two components were then calculated to evaluate whether both long-term environmental and biological changes were related to large-scale hydro-climatic forcing.

High correlations were found between both the EA pattern and NHT anomalies and the first PC from the PCA performed in the North Sea (Table 1; Fig. 6), revealing a synchronous influence of the two indices in this region. After accounting for temporal autocorrelation, the probability was however not significant at the traditionally-used probability level of 0.05. It is, however, well-known that this type of correction can be too conservative (Legendre and Legendre, 1998). The mathematical theory on tests of significance did not propose originally an appropriate level of significance (Tullock, 1970). The choice of what is considered to be the universal level of significance ($p = 0.05$) is, therefore, not based on mathematical theory. The most serious consequence of this arbitrary choice is that, in some circumstances, it may lead to the acceptance of the null hypothesis when it should be rejected (type II error). Beaugrand and Reid (2012) discussed this point in great details. Owing to the high value of the correlation ($r > 0.8$), explaining 64% of the total variance (48 original degrees of freedom) and because the strong reduction in the degree of freedom after accounting for temporal autocorrelation is also an information, we considered that the strong correlation between both NHT anomalies and EA pattern and the first PC was important to consider thereafter. Although the winter NAO index was significantly correlated to the first PC, a graphical examination emphasised that the relationship only explained 27% of the total variance, in contrast to both NHT anomalies and the EA pattern (Fig. 6). The second PC was only correlated positively with the AMO index (Table 1). A closer graphical examination showed that the relationship between the two variables was mainly related to their low frequency variability, as the high frequency variability was not in phase (Fig. 6d).

In the Northeast Atlantic, the first principal component was strongly positively correlated to NHT anomalies and the EA pattern. Here again, the probability was superior to the probability threshold of 0.05 ($p = 0.11$; Table 1). However because the correlation explained more than 60% of the total variance with an uncorrected degree of freedom of 48, we chose to consider these correlations thereafter. A graphical examination revealed that the correlation between these variables was primarily driven by their long-term changes (Fig. 6e). The second component was correlated positively with the AMO index (Table 1; Fig. 6h). The NAO had no influence on ecosystem changes in the Northeast Atlantic.

We represented in a plane the first two principal components that derived from the PCA performed in the North Sea and in the Northeast Atlantic (Fig. 7). We attributed for each observation a value corresponding to a large-scale hydro-climatic variable. These values were subsequently interpolated in the plane of the first two PCs and were represented by a colour scale to examine the relationships between long-term changes in the first two PCs and the large-scale hydro-climatic variable. These diagrams revealed that in both the North Sea and the Northeast Atlantic the positive values of the first PCs were explained by both the NHT and the EA pattern while positive values of the second PCs observed prior to 1962 and after the mid-1990s coincided with a positive phase of the AMO. The AMO was the only variable explaining the positive values of the second PCs. The analysis therefore suggested that the exceptional period after the mid-1990s is related to the synchronous positive forcing of NHT anomalies, the AMO and EA patterns. The anomalies observed during the period 1958–1962 were primarily due to the positive phase of the AMO and an absence of negative forcing by the NAO and the EA pattern.

4. Discussion

Comparative approaches are particularly sensitive methods to explore the mechanisms behind ecosystem responses to large-scale climate change (e.g. Megrey et al., 2009). Such approaches have been particularly promoted within the Global Ocean Ecosystem Dynamics (GLOBEC) programme and used to investigate how similar ecosystems (e.g. upwelling regions, Alheit and Bakun, 2010) respond to varying hydro-climatic forcing. At similar latitudes, seas may react differently to climate change due to location-specific characteristics such as basin depth and configuration, salinity and nutrient regimes, current patterns, and biotic features, including biogeographical setting, biodiversity and food-web organisation (Philippart et al., 2011). For example, whilst changes in open seas (e.g. the Northeast Atlantic) are more governed by the influence of atmospheric circulation on water stratification,

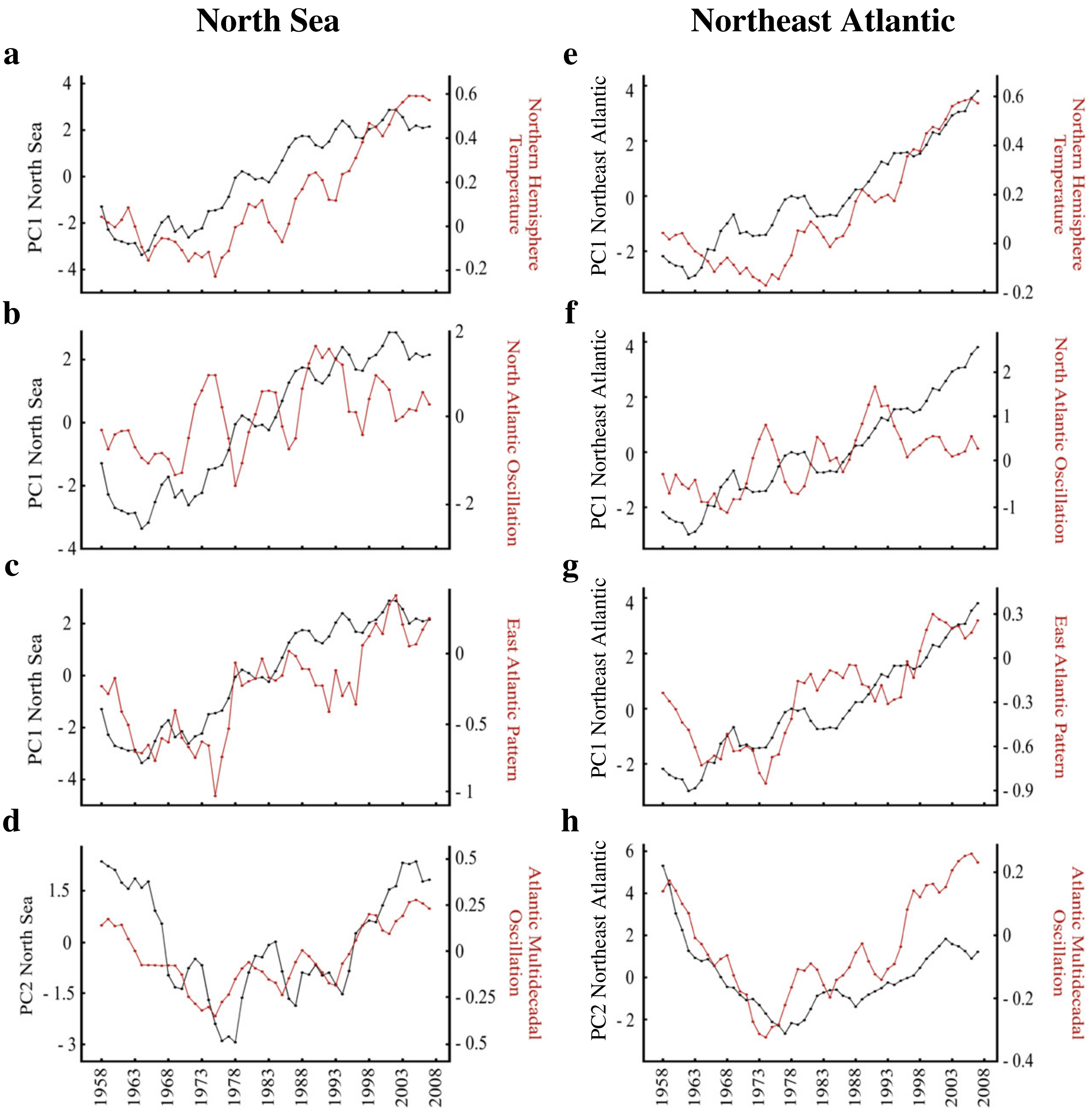

Fig. 6. Long-term ecosystem changes (principal components, in black) in both the North Sea (left panels) and the Northeast Atlantic (right panels) in relation to hydro-climatic forcing (in red). Variables were selected on the basis of Table 1.

enclosed seas such as the North Sea might be more affected by the influence of atmospheric circulation (wind and precipitation) via their effect on river runoff or oceanic inflow (Reid et al., 2003b). Our results suggest, however, strong similarities between long-term ecosystem changes in the North Sea and the Northeast Atlantic Ocean (see Fig. 5), which suggest (1) that a common atmospheric forcing has influenced these two regions and (2) that the processes by which climate manifests itself through the ecosystem are similar.

Many correlations between large-scale hydro-climatic indices and biological processes have been reported in the literature (e.g. Alheit and Bakun, 2010; Drinkwater et al., 2003; Hare and Mantua, 2000). Incorporating the characteristics of the atmosphere regionally or globally, large-scale indices can account for a significant part of the variance of an ecosystem and more than any single regional hydro-climatic variable (Drinkwater et al., 2003; Stenseth et al., 2003). One reason may be that such indices are usually related to a combination of several physical variables (Drinkwater et al., 2010). We found high correlations between long-term ecosystem changes and NHT anomalies, the AMO and to a lesser extent the EA pattern in both regions (Fig. 6, Table 1). However, not all correlations remained significant after accounting for temporal autocorrelation, at the classical probability threshold of $p = 0.05$. The absence of significance of the high correlations is related to the linearity of changes and the presence of monotonic trends in many time series. The effect of the year-to-year variability, used to be strong in the past in such time series (e.g. Beaugrand and Reid, 2003; Reid and Beaugrand, 2012), is now relatively small. Correlations suggest that the long-term variability of the state of the ecosystems located in the North Sea and the Northeast Atlantic is currently coincident with large-scale hydro-climatic forcings such as NHT anomalies, the AMO index and the EA pattern. The synchronous increases of these indices, which clearly accelerated in the mid-1990s, may explain the relative decline observed in the natural variability (i.e. seasons). The graphical examination of principal components (Fig. 7) indicated that both NHT anomalies and the

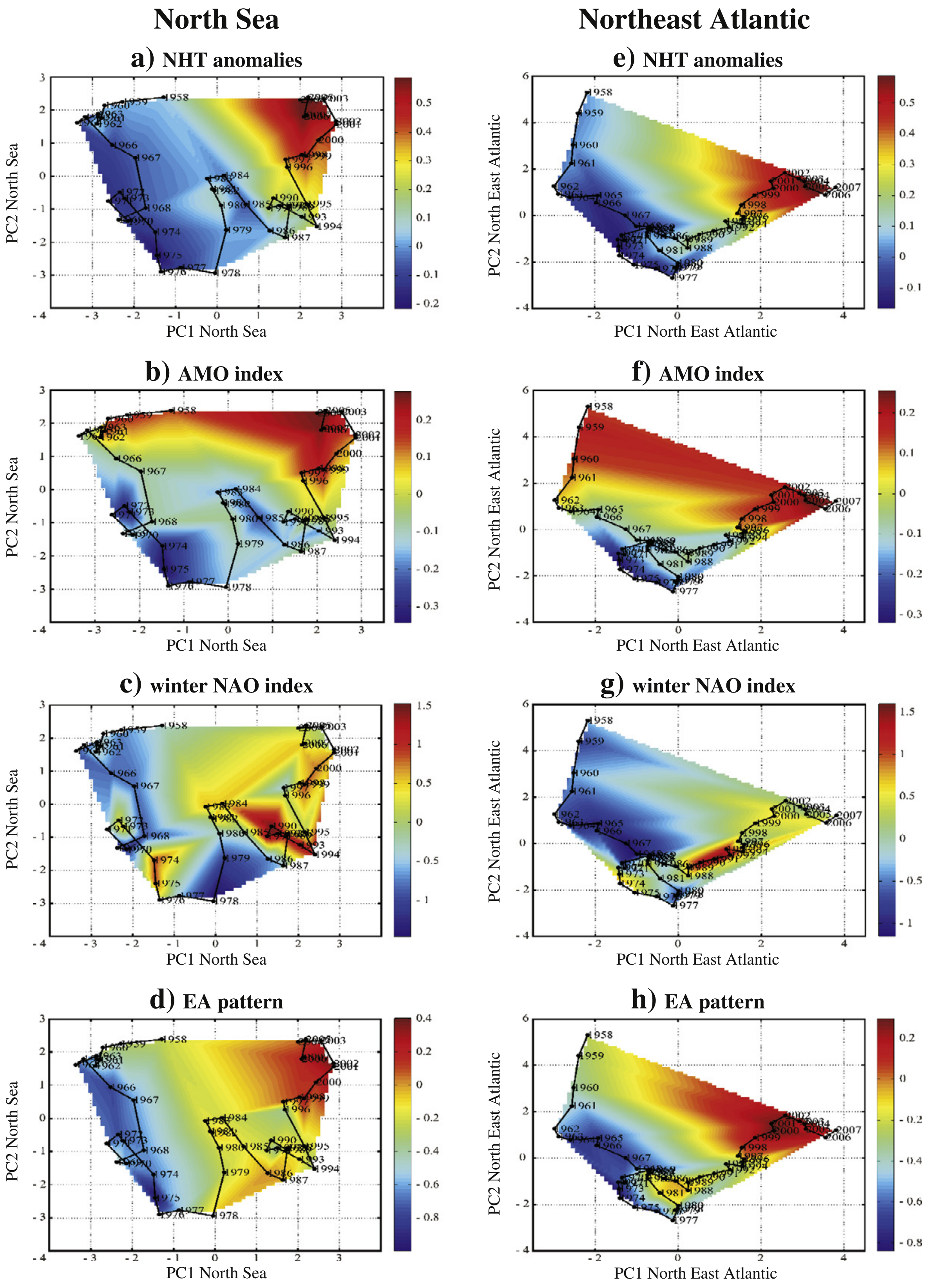

Fig. 7. Relationships between each large-scale hydro-climatic index and the first two PCs of the PCA performed for the North Sea (left panels) and for the Northeast Atlantic (right panels) (see Analysis 4). Relationships between the first two PCs of the PCA performed for the North Sea and (a) NHT anomalies, (b) the AMO index, (c) the winter NAO index, and (d) the EA pattern. Relationships between the first two PCs of the PCA performed for the Northeast Atlantic and (e) NHT anomalies, (f) the AMO index, (g) the winter NAO index, and (h) the EA pattern.

EA pattern had a strong influence after the mid-1990s on long-term changes in ecosystem states. Only the AMO can however explain ecosystem changes revealed by the second components (Fig. 7). Together these results allow us to understand that the first positive ecosystem (1958–1962) state often found in studies using CPR data (Beaugrand et al., 2009) is related to the end of the positive phase of the AMO whereas the new shift detected after the mid-1990s (e.g. Luczak et al., 2011) has been primarily driven by NHT anomalies and the EA pattern. Although the EA pattern has already been suggested to control the long-term changes in a British arctiid moth (Conrad et al., 2003), the effect of the EA pattern has rarely been investigated in the marine realm. Although often used in bioclimatology, the relationships between species or ecosystem shifts and the winter NAO index were weak and not constant through time (Beaugrand, 2012; Kimmel and Hameed, 2008). This could be due to the modest influence of the oscillation on the regional climatological indices of the region (Marshall et al., 2001). Beaugrand (2012) showed that the relationship between the state of the NAO and the subarctic species *C. finmarchicus* broke down during the mid-1980s at the time of the North Sea abrupt ecosystem shift.

Because we found strong correlations between the ecosystem state in both regions and large-scale hydro-climatic indices that have in turn a strong influence on sea surface temperature (see Fig. 1), our results suggest that temperature is the leading major process by which climate propagates through the ecosystem. We caution however that other parameters may be at work. These parameters include food (Lomolino et al., 2006), which may be measured by chlorophyll *a* concentration, nutrient concentration (Goberville et al., 2010; Sverdrup, 1953) and the structure of the water column influenced by winds (Reygondeau & Beaugrand, 2011a), to only cite a few. Long-term changes in sea surface temperature in the Northeast Atlantic sector have already been related to both NHT anomalies and the AMO index (Beaugrand et al., 2002; Edwards et al., 2013; Keenlyside et al., 2008) and to a lesser extent to the EA pattern (Msadek and Frankignoul, 2009). Although it is to some extent speculative to propose mechanisms by which climate might affect Northeast Atlantic ecosystem from a retrospective analysis such as ours, temperature might influence Northeast Atlantic ecosystems in four different ways. First at the individual scale, temperature affects metabolism, feeding, respiration, growth and reproduction (Mauchline, 1998; Peters, 1983; Portner and Knust, 2007). Second, temperature governs life history, survival, generation time and differential mortality of species. As they integrate environmental signals over generation time, species transfer potential perturbations to the next generation. Third, temperature drives the species composition and the average size of organisms within an ecosystem (e.g. projection of smaller primary producers in a warmer ocean; Moran et al., 2010) and modulates species interaction (Kirby and Beaugrand, 2009; Richardson and Schoeman, 2004). Fourth, temperature also alters the spatial distribution of species, communities and ecosystems (Longhurst, 2007; Reygondeau and Beaugrand, 2011b). Because plankton is highly sensitive to environmental changes (Reid and Edwards, 2001; Taylor et al., 2002), climate change may thereby have a considerable effect throughout the ecosystems (Richardson, 2009; Taylor et al., 2002).

In both systems, we observed gradual trends interrupted by more abrupt shifts detected *circa* 1976, 1987–1988 and 1996–2000 (see Fig. 5). The timing of these abrupt shifts coincided with what have been reported in the scientific literature (e.g. Beaugrand et al., submitted for publication; Luczak et al., 2011; Weijerman et al., 2005). We caution, however, that all ecosystem components did not react to these changes exactly at the same time. Furthermore, within each ecosystem unit, not all variables were associated to the change (Tables S1 to S5). It follows that only a small fraction of both the ecosystem components exhibited a shift during these periods. This fact has been often found in studies but rarely stressed. For example, Weijerman et al. (2005) in their analysis of the long-term changes of the North Sea ecosystem state that only a fraction of the variables examined exhibited a shift at the end of the 1980s. Beaugrand et al. (submitted for publication) showed that only 40% of plankton species exhibited a shift in the 1980s and at the end of the 1990s. This fraction of plankton species, probably located at the edge of their environmental niches is thereby more sensitive to temperature changes whereas other species located in the central part of their distributional range might buffer shifts in temperature (Beaugrand, 2012). It is also possible that some ecological variables respond instantly to large-scale forcing while changes in others may be either lagged or not detected (Weijerman et al., 2005).

The relationships between large-scale climatic phenomena and ecological processes may not be constant in time, revealing both the non-stationarity and nonlinearity between patterns of variability (Beaugrand, 2012; Kirby and Beaugrand, 2009). For example, the negative correlation between the NAO and *C. finmarchicus* noticed between 1962 and 1992 in the North Sea (Fromentin and Planque, 1996) collapsed after the mid-1980s. While this breakdown may be due to a slight east or northeast displacement of both NAO centres of action (Stenseth et al., 2004), this phenomenon could also be in part explained by the non-linear response of species to temperature change (Beaugrand, 2012). The effect of climate also depends upon the intensity of the climatic anomalies and their effects on the resilience of both biological and ecological systems. Both substantial forcings can be related to changes in the ecosystem state, while moderate forcing might have no effect (Goberville et al., 2010). For instance, Goswami et al. (2006) showed that the seasonal monsoon rainfall in Eurasia was modulated by the intensity of NAO events and its effect on the gradient of tropospheric temperature. Such threshold effects are beginning to be widely documented in all types of natural systems (Scheffer et al., 2001) and reflect a pronounced sensitivity of the response of many ecosystems to climate changes.

We show that two ecoregions, with distinct inherent specificity, have responded to climate change in a similar way. The magnitude of both environmental and biological changes observed is surprisingly important over the multi-decadal scale and the effect of year-to-year variability is small, indicating that these ecosystems are responding to strong hydro-climatic forcing that is operating at large spatial and temporal scales. Extrinsic parameters involved in their responses are large-scale hydro-climatic factors that locally control the thermal regime of the sea, thus suggesting that climate influences marine ecosystems through the effects of temperature on the physiology, species ecology and species interactions.

Acknowledgements

The authors are grateful to all past and present members and supporters of the Sir Alister Hardy Foundation for Ocean Science, whose continuous efforts have allowed the establishment and maintenance of the long-term CPR dataset. This is a contribution to the programme BIODIMAR. The survey depends on the owners, masters, and crews of the ships that tow the CPRs.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jmarsys.2013.05.008.

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