

Long-term changes in phytoplankton, zooplankton and salmon related to climate

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Abstract

Recently, large-scale changes in the biogeography of calanoid copepod crustaceans have been detected in the northeastern North Atlantic Ocean and adjacent seas. Strong biogeographical shifts in all copepod assemblages were found with a northward extension of more than 10° in latitude of warm-water species associated with a decrease in the number of colder-water species. These changes were attributed to regional increase in sea surface temperature. Here, we have extended these studies to examine long-term changes in phytoplankton, zooplankton and salmon in relation to hydro-meteorological forcing in the northeast Atlantic Ocean and adjacent seas. We found highly significant relationships between (1) long-term changes in all three trophic levels, (2) sea surface temperature in the northeastern Atlantic, (3) Northern Hemisphere temperature and (4) the North Atlantic Oscillation. The similarities detected between plankton, salmon, temperature and hydro-climatic parameters are also seen in their cyclical variability and in a stepwise shift that started after a pronounced increase in Northern Hemisphere Temperature anomalies at the end of the 1970s. All biological variables show a pronounced change which started after circa 1982 for euphausiids (decline), 1984 for the total abundance of small copepods (increase), 1986 for phytoplankton biomass (increase) and *Calanus finmarchicus* (decrease) and 1988 for salmon (decrease). This cascade of biological events led to an exceptional period, which is identified after 1986 to present and followed another shift in large-scale hydro-climatic variables and sea surface temperature. This regional temperature increase therefore appears to be an important parameter that is at present governing the dynamic equilibrium of northeast Atlantic pelagic ecosystems with possible consequences for biogeochemical processes and fisheries.

Keywords: climate change, Continuous Plankton Recorder, North Atlantic, North Atlantic Oscillation, plankton, salmon

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Introduction

Atmospheric concentration of carbon dioxide has risen from 280 ppm (parts per million) in 1750–367 ppm in 1999 (Intergovernmental Panel on Climate Change, 2001). Today's concentration has not been exceeded during the past 420 000 years (Petit *et al.*, 1999; Smith *et al.*, 1999) and it is likely that this rate of increase was unprecedented during the last 20 million years (Intergovernmental Panel on Climate Change, 2001). The effects of this increase in CO₂ concentration, associated with other anthropogenic greenhouse gases such as methane and nitrous oxide are

very likely to be responsible for the global increase in temperature seen over the last 50 years. Models predict that the increase in atmospheric greenhouse gases will continue during the 21st century leading to an increase in temperature ranging between 1.4 and 5.8 °C (Intergovernmental Panel on Climate Change, 2001).

Effects of both the increase in CO₂ concentration and global warming on ecosystems have just recently started to emerge in the scientific literature and many aspects of this influence are still poorly understood (Hughes, 2000). These may influence organisms in a direct way by acting on their physiology (e.g. photosynthesis, Keeling *et al.*, 1996; Myneni *et al.*, 1997) or on the phenology of species (e.g. seasonal cycle, Crick *et al.*, 1997; McCleery & Perrins, 1998). It may also impact biological systems in indirect

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ways by modifying abiotic factors involved in interspecific relationships (Kiesecker *et al.*, 2001; Pounds, 2001). This, in turn, may effect the spatial distribution of species and modify the whole community up to the ecosystem level (Beaugrand *et al.*, 2002).

In marine pelagic ecosystems, interpretation of the temporal variability of biological processes and identification of the main variables that drive the dynamic regime of marine ecosystems is complex. Indeed, many external forces ranging from the micro- to the mega-scale can influence the long-term variability of the marine biological environment. For example, long-term changes in the abundance and diversity of plankton or the community structure of pelagic ecosystems in the North Atlantic Ocean and adjacent seas have been linked to the mean intensity and direction of wind (Dickson *et al.*, 1988), the North Atlantic Oscillation (Fromentin & Planque, 1996; Beaugrand *et al.*, 2000; Beaugrand & Ibañez, 2002), the latitudinal position of the Gulf Stream north wall (Hays *et al.*, 1993; Taylor, 1995) and recently Northern Hemisphere temperature (Beaugrand *et al.*, 2002).

Changes in the abundance, diversity and composition of plankton, induced by modifications in the hydro-meteorological environment, may have pronounced consequences for higher trophic levels such as the Atlantic salmon *Salmo salar*. North Atlantic salmon stocks have declined, especially since 1990 (Mills, 2000). It is believed that this decline is a consequence of a reduction in the survival rate at sea as freshwater production seems to have been maintained in recent years (Hawkins, 2000). Processes behind the decline remain unclear as understanding of most aspects of salmon life at sea are still poor. Climate change may be an important factor as has recently been stressed for the Pacific salmon *Oncorhynchus nerka* (Finney *et al.*, 2000). Other works have reported significant relationships between salmon abundance and distribution and sea surface temperature (Reddin *et al.*, 2000). The aim of this study was to examine the extent to which changes in phytoplankton, zooplankton and salmon were related to climate and if similarities between all three trophic levels could be detected.

Materials and methods

Biological data

Plankton data used in this study come from the Continuous Plankton Recorder (CPR) survey. This monitoring programme was initiated in the North Sea in 1931 by Sir Alister Hardy (Hardy, 1926; Hardy, 1939). Sampling is carried out by a plankton recorder, which is towed typically at speeds between 10 and 20 knots behind voluntary merchant ships at a depth of about 6.5 m

(Warner & Hays, 1994). Data corresponding to the period 1948–2000 were used to investigate long-term changes in the spatial distribution of phytoplankton colour as an indicator of primary production. Phytoplankton colour is a visual index of chlorophyll based on the green colouration of the CPR filtering silk (Reid *et al.*, 1998). Long-term spatial changes in the distribution of some key zooplanktonic groups for salmon were also investigated. Both the total abundance of copepods (approximately inferior to 2 mm) and the abundance of the copepod *Calanus finmarchicus* were used as an indicator of secondary production. Euphausiids were utilized as they, and to a lesser extent *C. finmarchicus*, can represent a significant part of the diet of post-smolt salmon (Jacobsen & Hansen, 2000). Euphausiids identified in routine analysis include both adults and furciliars (Lindley, 1977). All stages of euphausiids can be eaten by post-smolts and to a lesser extent pre-adult salmon although no study has made any distinction between calyptopis, furciliars and adult Euphausiids.

Nominal catch of salmon in homewaters was used in this study as an estimate of salmon abundance (North Atlantic Salmon Conservation Organisation (2001), Table 2112). This table was then sorted to retain data representing the North East Atlantic from 14 locations.

Physical data

Temperature anomalies for the Northern Hemisphere (NHT) from 1958 to 1998 were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office (London, UK). Climate change in this study has the same meaning as that used in the Intergovernmental Panel on Climate Change (2001) report and may result as a consequence of natural internal processes (e.g. the effect of the North Atlantic Oscillation), natural external forcing (e.g. the influence of the Sun) or human-induced external forcing (e.g. increasing concentration in greenhouse gases in the atmosphere).

The winter North Atlantic Oscillation (NAO) index (Hurrell, 1995) for the period 1958–1999 was obtained from the internet site <http://www.met.rdg.ac.uk/cag/NAO/index.html>. The NAO is a basin scale alternation of atmospheric mass over the North Atlantic between the high pressures centred on the Azores and low pressures around Iceland. The index used here is based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. Both the winter (December to March) and monthly NAO indices were used.

Sea Surface Temperature (SST), from 1960 to 1997 were derived from the Comprehensive Atmosphere Data Set (COADS, Woodruff *et al.*, 1987). This is a global oceanographic data set, which includes a statistical summary of

many climatic parameters for each month of each year using 1° latitude \times 1° longitude boxes.

Numerical procedures and statistical analyses

About 180 000 CPR samples were analysed in this study. Five steps were needed to produce long-term maps and to identify the main patterns of change in the data.

Step 1: The CPR database was reorganized to allow each sample to be located in space and time.

Step 2: Latitude and longitude were transformed to Lambert co-ordinates, which allowed surfaces on the map to be proportional to actual surfaces over the survey area and thus to avoid a strong distortion of distance on the map (Planque *et al.*, 1997).

Step 3: As the CPR sampling is also irregular in time (e.g. samples can be collected at any time of a day or night for any month or year), spatial interpolations were performed for each year, two-month period and for daylight and dark periods using the function given in Beaugrand *et al.* (2001, Fig. 1). In each case, interpolation by the inverse square distance method was realized on a grid of 50×50 nautical mile (same grid for SST) pixels using a search radius of 300 nautical miles. The number of neighbours was fixed between 5 and 15. Sea surface temperature data were interpolated using the same procedure with no distinction for day and night observations. The spatial interpolation may be influenced by plankton patchiness (Tsuda *et al.*, 1993). However, the number of neighbours considered in this study is sufficiently high to prevent a strong influence of this feature in interpolated data and the production artificial structures. Beaugrand & Edwards (2001) showed a strong reduction of the unexplained variance of diversity estimation of calanoid copepods when five CPR samples were considered. This value corresponds to the minimum of neighbours used in this study and also in other works (Planque *et al.*, 1997; Beaugrand & Ibañez, 2002). Furthermore, the use of principal component analysis allowed reduction of its influence by only considering the major source of variability.

Step 4: The annual mean was calculated and maps were rearranged in a new matrix with in column the abundance of a taxon for each year and in row the geographical pixels. Two missing data (out of 12) were permitted in the calculation of the annual mean. This rate was fixed by trial and error. The resulting annual mean matrix included missing values for some pixels.

Step 5: The abundance data in the annual mean matrix were transformed using the function $\log_{10}(x+1)$ (Colebrook, 1975). Then, a PCA (based on an algorithm that takes into account missing data, Bouvier, 1977) was performed on each correlation matrix (about 730×730

non missing pixels) with the double objective of identifying major long-term changes (examination of principal components) and locating their geographical patterns (mapping of eigenvectors). A maximum of 10 missing data points in the temporal series was permitted. This rate was fixed by simulation. The PCAs performed on matrices with different levels of missing data showed similar conclusions.

A similar procedure was applied to analyse sea surface temperature. The first two eigenvectors and principal components (PCs) of the biological variables were related to the winter NAO index, NHT anomalies and to the first two PCs of the analysis of Sea Surface Temperature (SST). Relationships between principal components and large-scale hydroclimatic features and long-term changes in the biological environment were also investigated by correlation analysis. Probabilities were calculated both with and without the consideration of temporal autocorrelation. Box & Jenkins (1976) autocorrelation function modified by Chatfield (1996) was used on each pixel. Using the Chelton (1984) formula, a correction was applied as per Pyper & Peterman (1998) who showed that this type of correction gave better results than the Garret & Petrie (1981) method and more stable results than the Kope and Botsford's method.

In order to represent graphically changes between climatic and biological parameters cumulative sums were applied (Ibañez *et al.*, 1993; Beaugrand *et al.*, 2000). Firstly, each value of the series is subtracted by a reference value (here the mean). Secondly, the residuals are pooled progressively. This cumulated function is very sensitive to changes of the local mean values along the series (Ibañez *et al.*, 2002).

Split moving-window boundary analysis (SMW, Webster, 1973) was applied to detect temporal discontinuities in the univariate time series. The principle of this method is simple and can be summarized in four steps. (1) A window of even-numbered size is introduced at the beginning of the time series. (2) This window is divided into two half-windows. (3) An association coefficient is used to evaluate the differences between both time periods. Here, the absolute value of the difference between the average of both windows was retained and was tested using a Kruskal–Wallis test. (4) The window is then moved from year to year, repeating steps 2 and 3 until the end of the time series is reached. Results may change as a function of the size of the window (Webster, 1973). So, different sizes of window were tried, but only one will be presented to limit the number of figures.

The Eigenvector Filtering (EVF) method, also known as Principal Component Analysis of Processes (Ibañez & Etienne, 1991) or Singular-Spectrum Analysis (Vautard *et al.*, 1992), was applied to (1) decompose the time series,

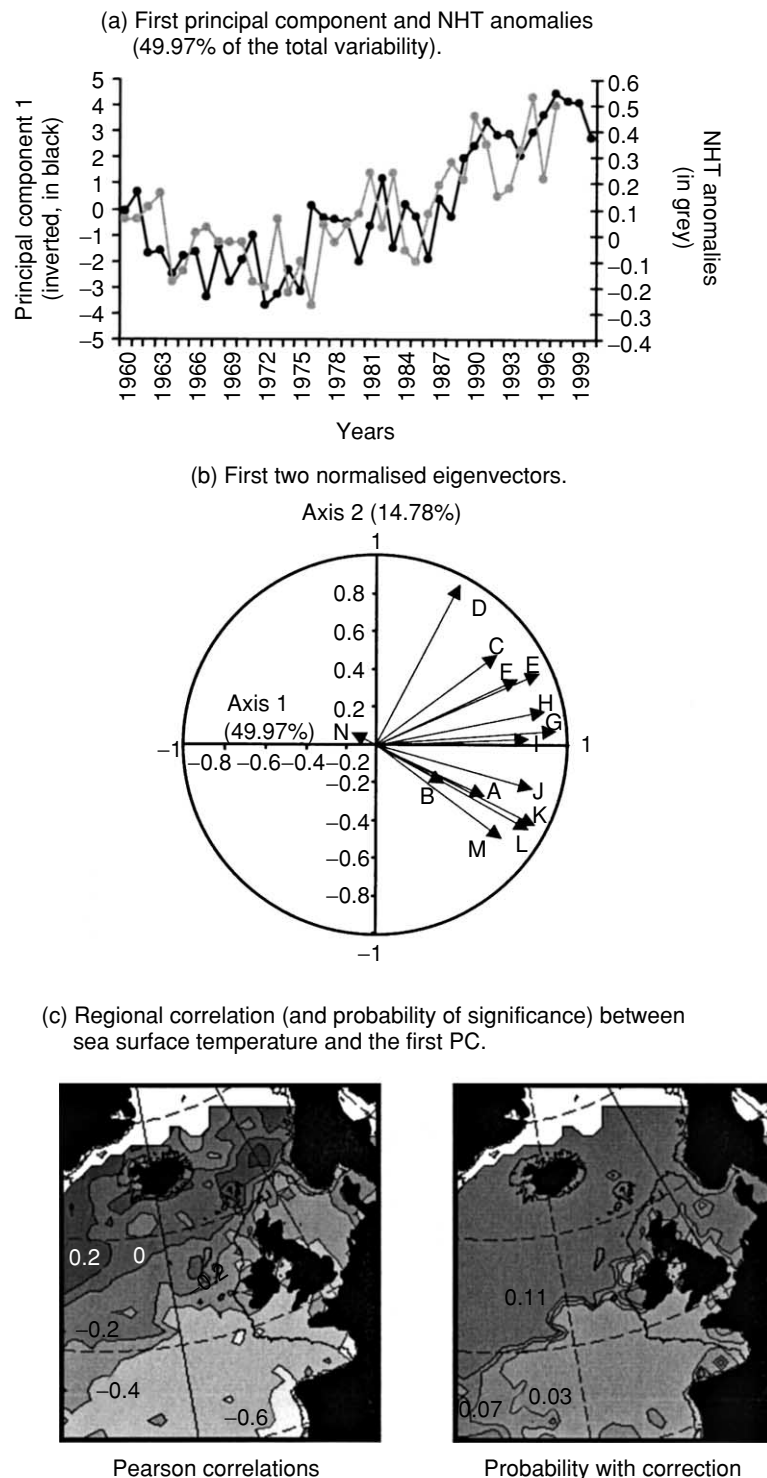


Fig. 1 A principal component analysis of long-term changes (1960–2000) in the nominal catch of salmon in homewaters of the eastern Atlantic. (a) Long-term changes in the first principal component (inverted, in black) and NHT anomalies (in grey). (b) Dispersion diagram of the first two normalized eigenvectors. (c) Pearson correlation coefficient (and its probability) between sea surface temperature and the first principal component. A: France Total; B: Iceland Wild Total; C: Ireland Second or Multi Sea Winter; D: Ireland First Sea Winter; E: Ireland Total; F: Northern Ireland Total; G: Scotland Second or Multi Sea Winter; H: Scotland First Sea Winter; I: England and Wales Total; J: Spain Total; K: Norway Total; L: Norway Second or Multi Sea Winter; M: Norway First Sea Winter; N: Sweden West Total.

(2) quantify the different types of variability, (3) remove the long-term trend and (4) further examine relationships between biological and hydro-climatic variables. This univariate technique is robust for short time series (the case in this study). The principle of this method can be summarized in three steps. (1) The time series is lagged with itself from one year to Δt years and then transformed into an autocovariance matrix (also called a Toeplitz matrix). For all time series after examination of the autocorrelation functions, Δt was fixed to 11 years. (2) Eigenvalues and eigenvectors are then calculated. The original values of the time series can be reassessed from a limited number of principal components. As all first eigenvectors revealed the long-term trend, only series reassessed from the second and third eigenvectors, as well as the residual variability (values of the original time series subtracted by the series reassessed using the first three eigenvectors), are presented. (3) The gain function (Ibañez & Etienne, 1991), which is the ratio of the spectrum of the original on the reassessed time series, was calculated to identify periods that were emphasized by the decomposition. The algebra of the method is fully presented in Ibañez & Etienne (1991) and Vautard *et al.* (1992). All methods used in this study were programmed using the MATLAB language.

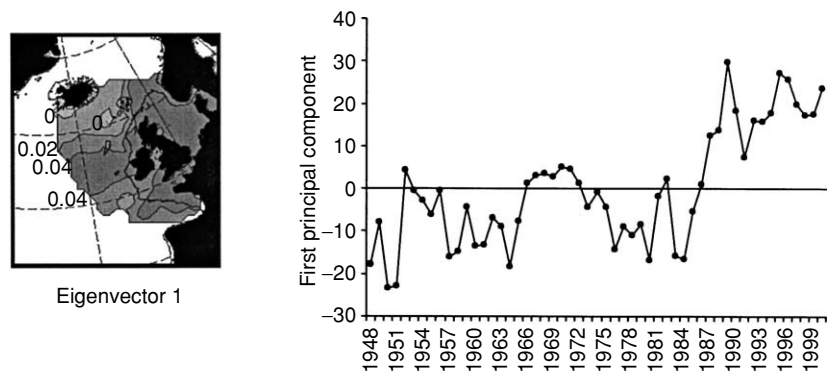
Results

Long-term changes in salmon and plankton

Long-term changes of salmon (as a principal component, Fig. 1(a)) were significantly correlated negatively ($r = -0.72$, $P < 0.0001$) to NHT anomalies and the relationship was still significant after correction of the probability to account for temporal autocorrelation ($P < 0.05$; correlation with the winter NAO index: 0.34, not significant). As nearly all variables related to the first principal component were positive on the dispersion diagram of the first two eigenvectors (Fig. 1(b)), this indicated that there was a negative relationship between salmon catch in homewaters and NHT anomalies for many North East Atlantic countries. A negative correlation between Sea Surface Temperature (SST) and the first principal component was detected approximately south of a latitude crossing Scotland (Fig. 1(c)).

Long-term changes in phytoplankton colour showed a slight decrease until the mid-1980s and then a sharp increase mainly in the North Sea and the oceanic region west of the British Isles between 50 and 58°N (Fig. 2(a)). An increase in phytoplankton colour until a maximum in 1955 was identified in the subarctic gyre south of Iceland

(a) First eigenvector and principal component (36.81%).



(b) Second eigenvector and principal component (13.07%).

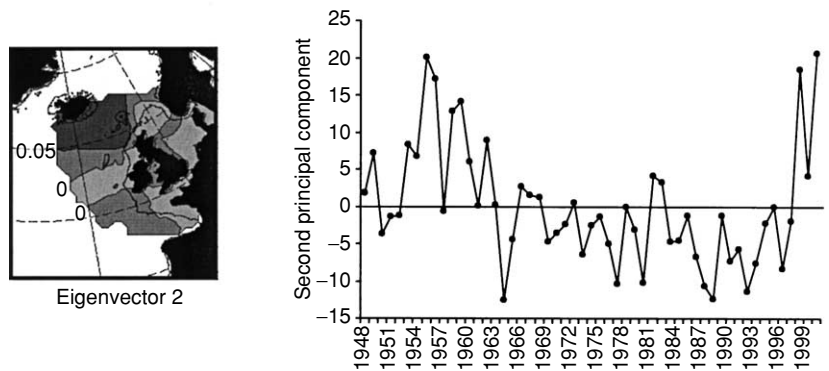


Fig. 2 Long-term spatial changes in phytoplankton colour. Principal component analysis on the correlation matrix geographical pixels \times geographical pixels. First (a) and second (b) eigenvectors and principal components are indicated.

followed by a continued decrease until the mid-1990s (Fig. 2(b)). This pattern reversed after 1996 with a strong increase in phytoplankton colour. Long-term changes in the abundance of total copepods, *C. finmarchicus* and euphausiids and sea surface temperature (SST) (for areas approximately corresponding to those identified by eigenvector 1 of the PCA performed on phytoplankton colour) and large-scale hydro-meteorological variables are presented in Fig. 3. All principal components reflect positively the abundance of species. Each principal component of the biological variables representing the North Sea, regions around the British Isles and/or to a lesser extent the eastern part of the North Atlantic Drift

Province (Longhurst, 1998) significantly covaried (positively for the abundance of small copepods, negatively for other biological variables) to both the first PC of SST and NHT anomalies (Table 1). It should also be noted that only one significant correlation was detected with the winter NAO index.

Relationships between biological and hydro-climatic changes

Cumulative sums (Fig. 4) performed on both biological and physical time series clearly showed a positive covariation between both the total abundance of copepods

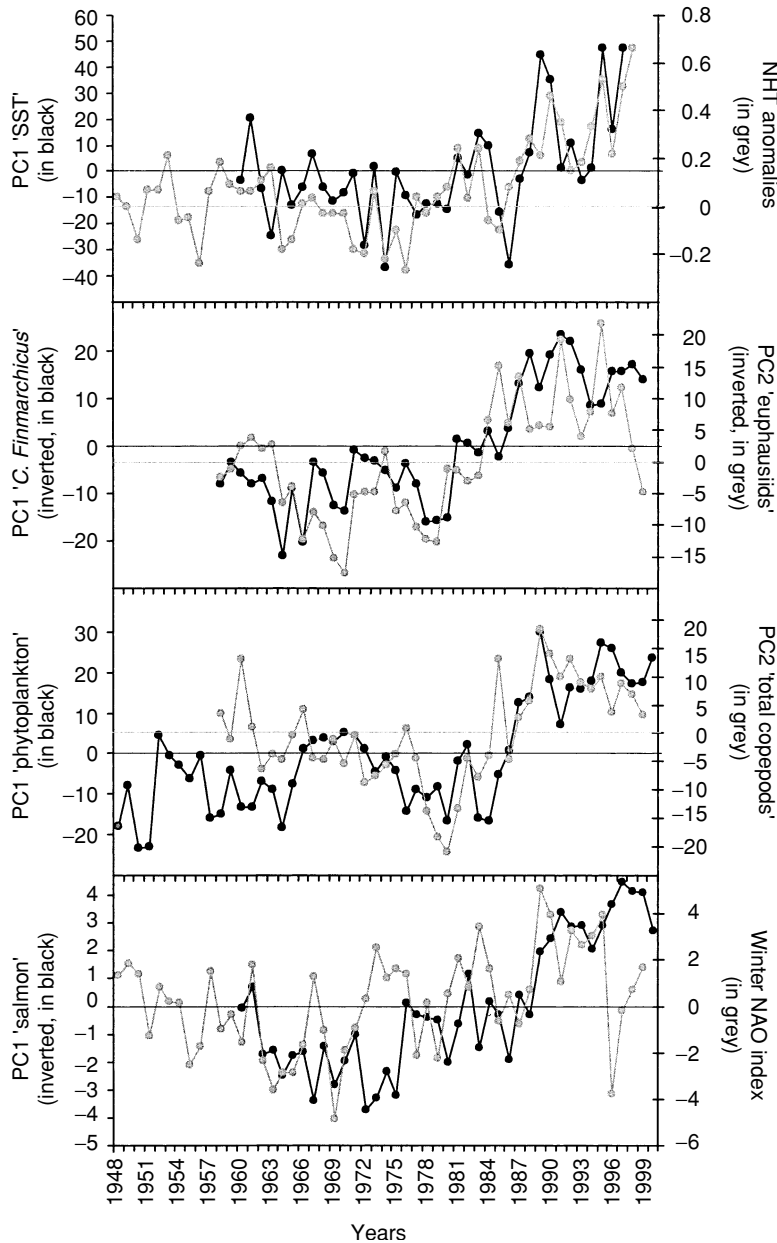


Fig. 3 Long-term changes in biological variables, sea surface temperature and large-scale hydro-climatic variables. PC1: first principal component. PC2: second principal component. Areas related to principal components correspond approximately to the area exhibited by eigenvector 1 in Fig. 2.

Table 1 Correlations between biological and physical variables

Biological variables	Areas	PC1 'SST'	PC2 'SST'	Winter NAO index	NHT anomalies
PC1 'colour'	1 + 2	0.54**	-0.21	0.27	0.57**
PC2 'colour'	3	0.00	0.28	-0.13	0.02
PC1 'copepods'	2	-0.24	0.35	-0.19	-0.36
PC2 'copepods'	1	0.52**	-0.05	0.29	0.43
PC1 ' <i>C. finmarchicus</i> '	1 + 2 (north)	-0.51**	0.44	-0.52*	-0.66*
PC2 ' <i>C. finmarchicus</i> '	3	-0.22	-0.27	0.05	-0.21
PC1 'euphausiids'	1 + 2 + 3	-0.23	-0.28	0.05	-0.13
PC2 'euphausiids'	1	-0.42*	0.21	-0.39	-0.56*
PC1 'salmon'	1 + 2	-0.63**	0.17	-0.39	-0.72**
PC2 'salmon'	1 + 2	-0.29	-0.06	-0.08	-0.23

Probabilities after correction for temporal autocorrelation are indicated. *, $0.1 > P > 0.05$; **, $0.05 \geq P \geq 0.01$. 1, North Sea; 2, eastern part of the North Atlantic Drift province (Longhurst, 1998); 3, Atlantic Arctic and Subarctic Provinces (Longhurst, 1998). PC1 'SST' was related to an oceanic area south of 50°N, around the British Isles and in the North Sea. PC2 'SST' was related to the Atlantic Arctic Province of Longhurst (1998).

and phytoplankton colour and physical variables while the other biological variables showed a negative correlation with those hydro-climatic variables. However, dispersion diagrams (Fig. 5) demonstrated that superimposed on the linear correlation detected between nearly all variables and NHT anomalies, a stepwise change occurred for all variables during the mid-1980s. Large discontinuities were detected for Euphausiids after circa 1982, for total copepods after circa 1984, phytoplankton colour and *C. finmarchicus* after circa 1986, and for salmon after circa 1988 (Fig. 6). The change corresponded for phytoplankton colour and the total abundance of copepods to an increase in abundance while for *C. finmarchicus*, euphausiids and salmon, this change corresponded to a decrease (Fig. 3). Here also, peaks of maximal biological change seemed to be more in correspondence with the peak of maximal variation for Northern Hemisphere Temperature anomalies detected around 1987 than with the NAO, which occurred slightly after circa 1988. All biological and physical changes that appeared during the 1980s led to an exceptional period (1987–1997) as demonstrated by a cluster analysis performed on biological and physical variables used in Fig. 3 (Fig. 7).

Variability explained by the previous analyses was mainly evident at low frequency. The consideration of temporal autocorrelation in the calculation of the probability of correlation coefficient assures however, that the results were robust. We further examined the relationships between biological and hydro-climatic variables by decomposing the time series of every variable represented in Fig. 3. The first eigenvector detected the long-term variability in all time series. This low-frequency variability for biological variables represented between 51.37% (PC2 'copepods') and 74.96% (PC1 'salmon') of

the total variance of the time series (Table 2). For hydro-climatic variables, the long-term trend was much less important (between 31.11 and 48.64%). This result suggests that biological variables have more 'memory' than physical parameters. The second eigenvector identified a pseudo-cycle of 14–15 years for biological variables. Caution should be applied to this result as only two cycles can be visualized in a short time series. This pseudo-cycle is interpreted here as influenced by the stepwise increase in the mid-1980s and may also reflect the long-term trend of the time series. Residual variance related to the other sources of variability is therefore weak for biological variables, ranging from 13.88% for *C. finmarchicus* to 21.90% for total copepods. The 14–15 years cycle is not observed for hydro-climatic variables, which have, although statistically significant (Fig. 6), a less pronounced change during the 1980s. Instead, those variables exhibited a cyclical variability between 6 and 11 years. All variables presented a cyclical variability of 8–9 years (third axis of all EVF decompositions, Table 2). Much more residual variability remains for hydro-climatic variables (between 32.87% for NHT anomalies and 41.11% for the NAO index).

Correlation analysis between the cyclical variability of biological and hydro-climatic variables led to the same conclusions as previous analyses done on the original time series (Table 3, Fig. 8). However, the influence of the NAO on copepods is detected at this scale in addition to the covariation between this atmospheric oscillation and the abundance of *C. finmarchicus*. The covariation between the first principal component of SST and NHT anomalies is reinforced while an influence of the NAO on SST is also detected (Fig. 8). When year-to-year variability is considered (residual variability) no covariation

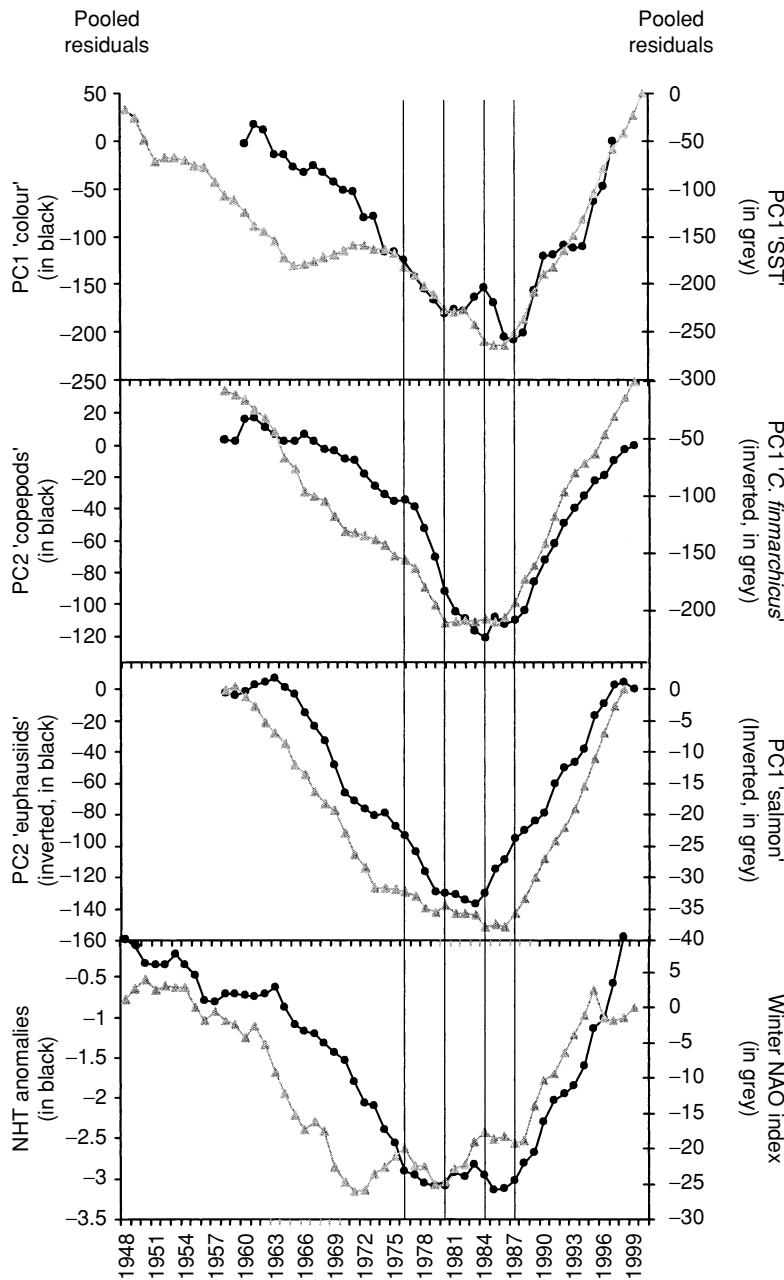


Fig. 4 Chronological series of biological and hydro-climatic variables after cumulative sums application. PC1: first principal component. PC2: second principal component.

between biological and hydro-climatic variables is found with the exception of the correlation between salmon and NHT. Thus, between 78 and 86% of the variance of the biological time series are explained in this study. A positive correlation between the NAO and SST is detected on a year-to-year scale (Table 3).

Long-term changes in the hydro-climatic environment of the Eastern North Atlantic Ocean

In order to understand how large-scale hydro-climatic processes may have influenced these three trophic levels,

we calculated correlations between long-term changes in monthly SST and both the winter NAO index and monthly NHT anomalies. The winter NAO index was used instead of monthly NAO indices as the NAO is primarily a winter phenomenon (Dickson & Turrell, 2000). Correlations were calculated for two periods: 1960–1978 and 1979–1997. These two periods were selected on the basis of results from Fig. 6 (discontinuity detected at the end of the 1970s for NHT anomalies) and as characterising prolonged phases of predominantly negative and positive NAO (Fig. 9(a)), a shift to high positive NHT anomalies after 1978 (Fig. 9(b)) and

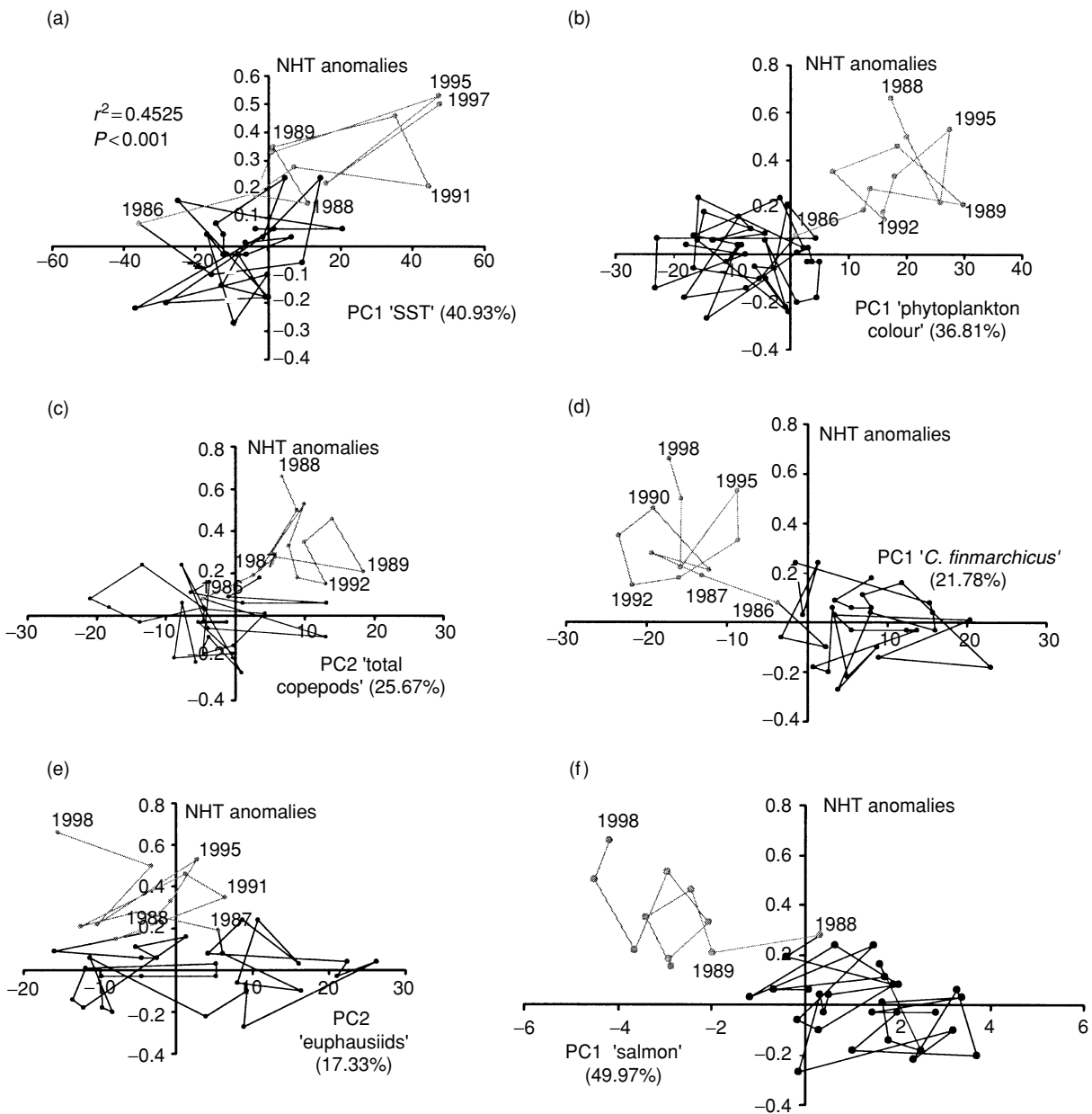


Fig. 5 Dispersion diagrams between NHT anomalies and the first principal component for (a) SST, (b) the first principal component for phytoplankton colour, (c) the second principal component for total abundance of copepods, (d) the first principal component for *C. finmarchicus*, (e) the second principal component for euphausiids and (f) the first principal component for salmon. Principal components were selected to represent regions (oceanic areas south of 50°N, an area around the UK and the North Sea) where SST has increased (Beaugrand *et al.*, 2002). Changes in the abundance of biological variables were correlated to SST (Table 1). The correlations between NHT anomalies and the first principal component for SST are indicated. Probabilities were corrected for temporal autocorrelation. Other correlation coefficients can be found in Table 1.

pronounced changes in calanoid copepod composition that occurred after circa 1978 (Beaugrand *et al.*, 2002). The two selected periods had an equal number of years (19). The relationship between the winter NAO and SST was slightly strengthened after 1978 (Fig. 9(a)). With NHT anomalies (Fig. 9(b)), a clear change in the

correlation pattern between both periods is found. In the second period a positive relationship with SST is detected in the eastern North Atlantic Ocean south of 52°N, around the British Isles and in the North Sea. Pixel maps (Fig. 10) show the number of months for which the probability of a correlation between the NAO

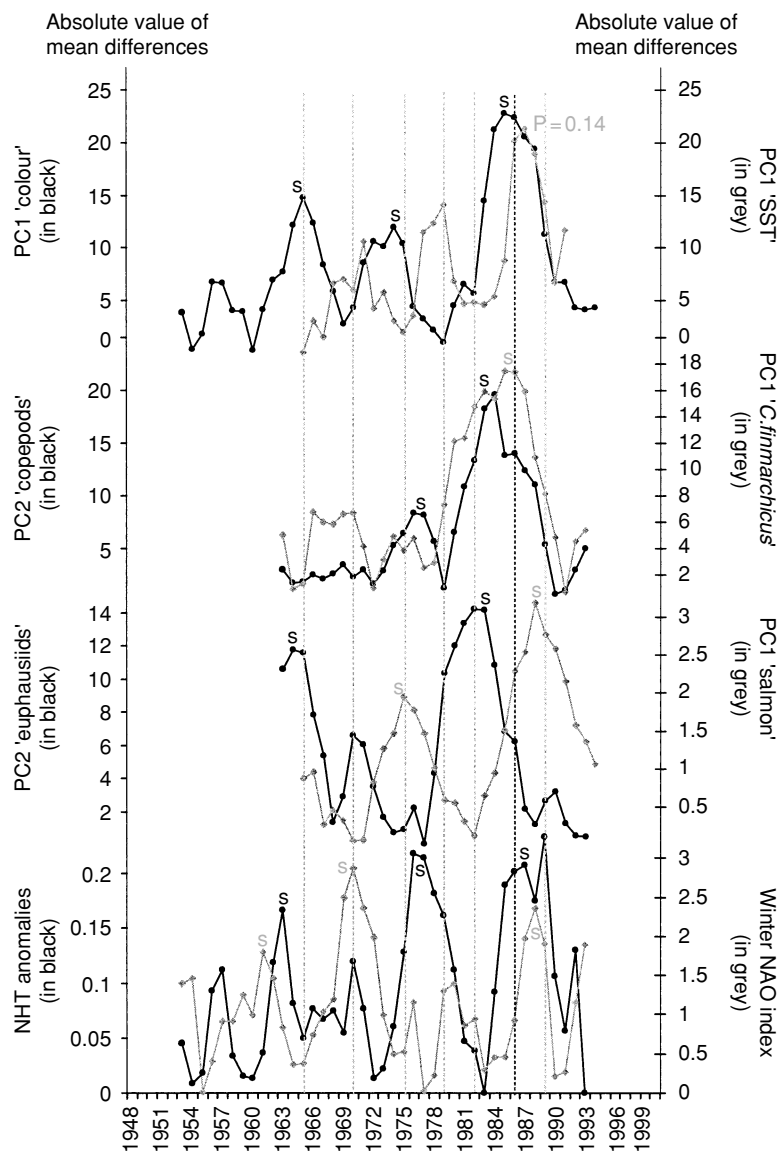


Fig. 6 Results of split moving-window boundary analysis performed on each biological and hydro-climatic variable displayed in Fig. 3, using a window size of 12 years (half-window size of 6 years). S: peak having a significant probability $P < 0.05$. See Materials and methods.

and NHT anomalies and monthly SST was inferior to 10%. For the NAO index (Fig. 10a), this slightly increased during the second period over the North Sea (positive correlation) and the subarctic gyre (negative correlation). However for NHT anomalies (Fig. 10b), while no pattern of significant correlation was found for the first period, a complete change occurred during the period 1979–1997 and it is clearly seen that NHT anomalies and SST covaried positively for many months in the eastern part of the North Atlantic, around the British Isles and in the North Sea. In the North Sea, this influence seems even to be stronger than that of the NAO.

Figure 11 shows the number of pixels with a significant correlation (< 0.1 after correction to account for temporal autocorrelation) between both the NAO and NHT anomalies and SST for each month and both

periods. The spatial coverage of correlations between the winter NAO index and SST did not change in autumn and winter but increased in spring and summer (Fig. 11(a)). For NHT anomalies, the spatial coverage of correlations strongly increased during the second period in autumn, winter and spring, but not in June–July (Fig. 11(b)).

Discussion

This study provides evidence that long-term changes in three trophic levels in the northeastern North Atlantic and the North Sea may be linked to climate change. Although dispersion diagrams indicate that other processes such as oceanographic episodic events described in Edwards *et al.* (2001) and Edwards *et al.* (2002) may

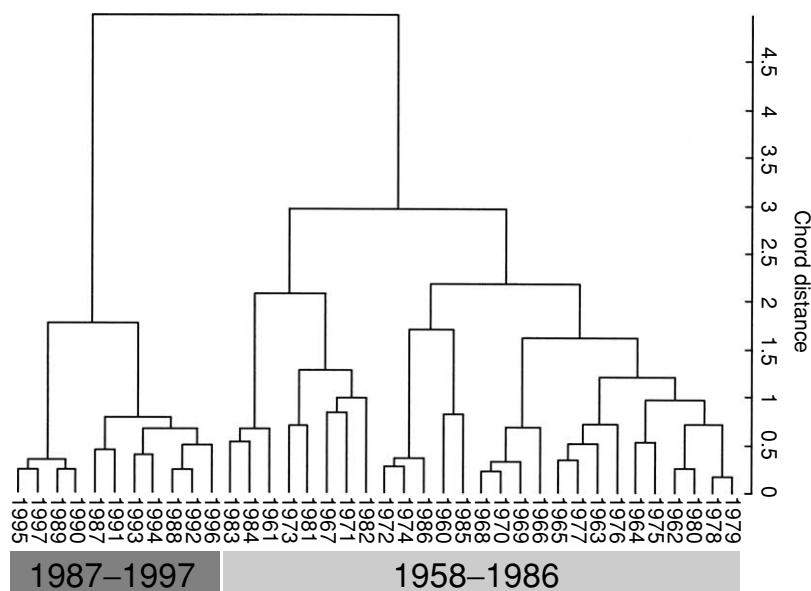


Fig. 7 Dendrogram of the cluster analysis performed on variables displayed in Fig. 3 for the period 1960–1997. Two periods are distinguished: 1960–1986 and 1987–1997.

Table 2 Summary of the decomposition of the temporal changes in biological and hydro-climatic variables by eigenvector filtering

Biological variables	First axis		Second axis		Third axis		Residual variability (estimation)
	Variability	EV1	Variability	EV2	Variability	EV3	
PC1 'colour'	LTD	60.81%	14.28	13.37%	8.33	7.74%	18.08%
PC2 'copepods'	LTD	51.37%	14.28	19.42%	8	7.32%	21.90%
PC1 ' <i>C. finmarchicus</i> '	LTD	71.10%	14.28	10.70%	8	4.32%	13.88%
PC2 'euphausiids'	LTD	59.35%	15.38	15.55%	8.69	5.83%	19.26%
PC1 'salmon'	LTD	74.96%	15.38	5.72%	8	4.59%	14.73%
PC1 SST	LTD	31.12%	6.45	17.84%	9	15.97%	35.07%
Winter NAO index	LTD	32.08%	10	13.91%	8.65	12.90%	41.11%
NHT anomalies	LTD	48.64%	11.11	9.27%	8.7	9.22%	32.87%

LTD, long-term trend; EV, eigenvector.

Table 3 Correlations between biological and hydro-climatic variables reconstructed by eigenvector filtering using both the second and third eigenvectors

Biological variables	Third eigenvector			Residual variability		
	NHT (8.7)	NAO (8.6)	SST PC1 (9)	NHT	NAO	SST PC1
PC1 'colour' (8.3)	0.62*	-0.26	0.32	0.00	0.11	-0.02
PC2 'copepods' (8)	0.05	0.42*	0.29	-0.22	0.01	0.14
PC1 ' <i>C. finmarchicus</i> ' (8)	-0.52*	-0.61*	-0.64*	-0.02	-0.08	-0.09
PC2 'euphausiids' (8.7)	-0.41*	0.00	-0.18	0.06	0.06	0.00
PC1 'salmon' (8)	-0.30	0.16	-0.46*	-0.33*	-0.02	0.12
NHT	1			1		
NAO	0.14	1		0.23	1	
SST PC1	0.53*	0.35*	1	0.16	0.61*	1

The number of years per cycle is indicated in brackets. *, Probability $P < 0.05$. Periods emphasized by the decomposition are indicated in brackets.

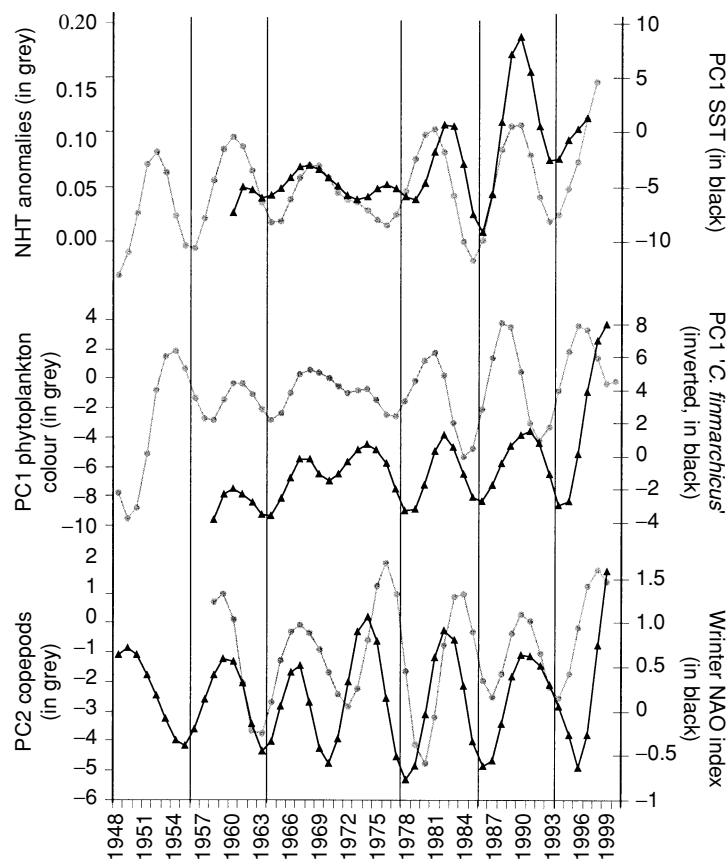


Fig. 8 Reconstructed time series of some biological and hydro-climatic variables (Fig. 3) from eigenvector filtering using the third eigenvector and principal components (Table 3). Vertical lines are added to facilitate the comparison of different time series.

temporarily reduce or mask the link between NHT anomalies and plankton (Fig. 5(e)), the relationship between salmon and NHT anomalies is particularly strong. Even though the NAO may have played a role in influencing this increase in temperature (Corti *et al.*, 1999), a significant correlation between biological variables and this large-scale climatological index was only found for *C. finmarchicus*. This result is particularly robust when low-frequency variability is considered. When the 8-year cyclical variability of all variables is considered, the results suggest a coincidence of high values of the NAO (possibly with a lag) with high values of both NHT anomalies and SST and biological variables (e.g. high for abundance of copepod or low for *C. finmarchicus*), although correlations were not significant in all cases. A strong positive covariation between this atmospheric oscillation and SST was also detected on a year-to-year scale, which was not noted in Beaugrand *et al.* (2002).

In addition to the similarities observed between the low-frequency (long-term) variability of the biology and NHT anomalies, all time series show a pronounced change during the 1980s, which started after circa 1982 for euphausiids, 1984 for total copepods, 1986 for *C. finmarchicus* and phytoplankton colour and 1988 for salmon. The first hypothesis proposed to explain this

difference in timing is that many species react differently to climate change depending upon the particular threshold values of their physiological processes or their life history (Walther, 2001). Another hypothesis, not exclusive of the first one, may be that the spatial centre of distribution of organisms is not exactly the same. However, when this effect is removed, we still observe differences in timing (Beaugrand & Ibanez, unpublished data). The delay detected between plankton and salmon does not necessarily mean that a trophic cascade or bottom-up biological control governs salmon abundance. The delay observed for salmon may be explained by their return to homewater rivers usually between one year for grilse (first sea winter fish) and three years (multi-sea winter fish) (Hutchinson & Mills, 2000). These major biological shifts followed a pronounced change in NHT anomalies at the end of the 1970s and approximately coincided with a stepwise change in NHT anomalies after circa 1987, then followed by a shift in the winter NAO index after 1988. Considering all biological parameters, these changes led to an exceptional period (1987–1997) in a 52-year time interval. These results justify why Reid *et al.* (2001) called this change a regime shift in the North Sea. This shift may also reflect a non-linear response of pelagic ecosystems to climate change (Scheffer *et al.*, 2001) as

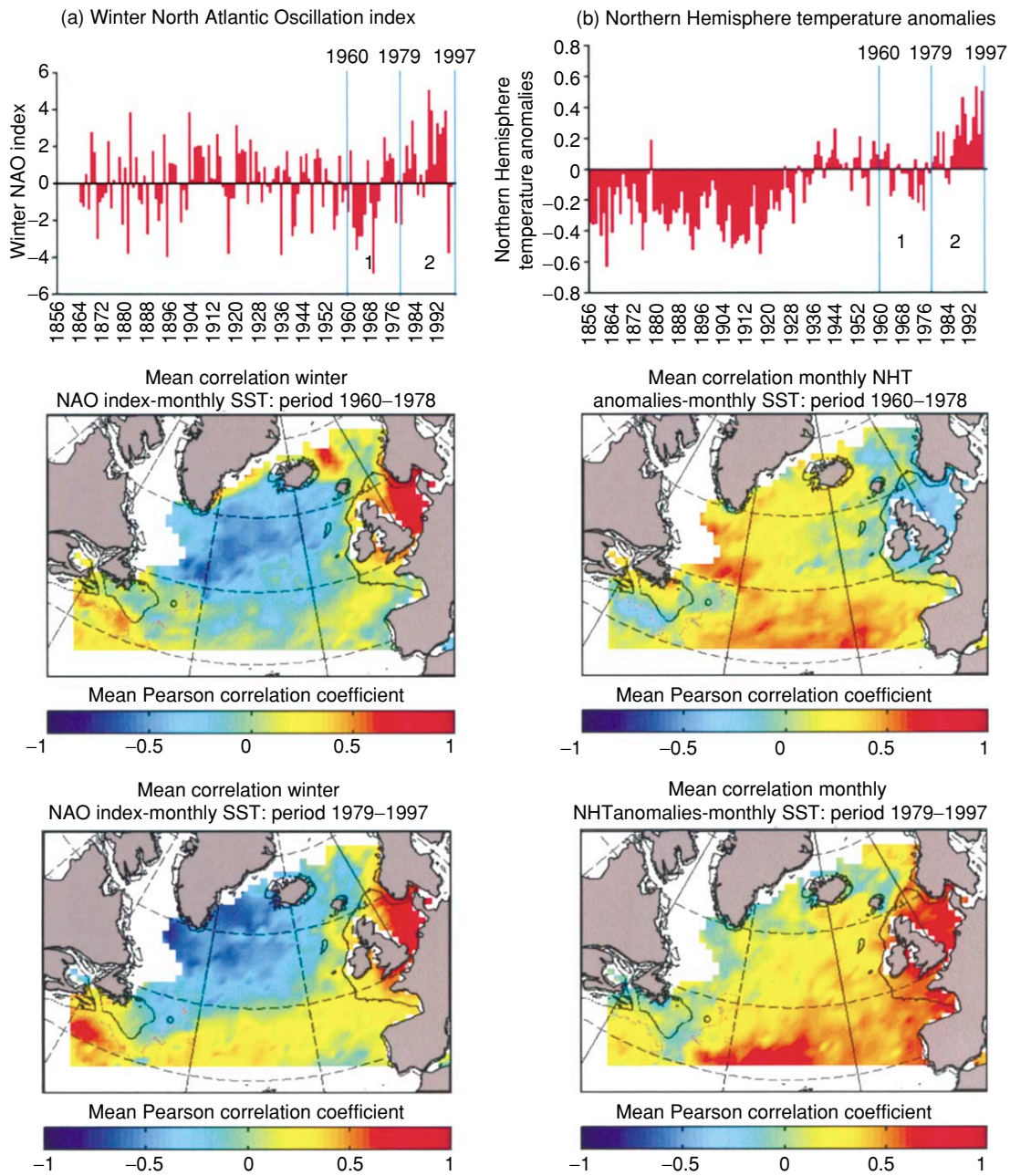


Fig. 9 Long-term changes in the winter North Atlantic Oscillation (NAO) index (a) and monthly Northern Hemisphere Temperature (NHT) anomalies (b). Maps of correlations were produced for each month between the winter NAO index and monthly SST. The left panel presents the average of the monthly correlation maps for the time period 1960–1978 (19 years) and the time period 1979–1997 (19 years). Maps of correlations were also produced for each month between monthly NHT anomalies and monthly SST. The right panel presents the average of the monthly correlation maps produced for the time period 1960–1978 (19 years) and the time period 1979–1997 (19 years).

the statistically significant discontinuities are less pronounced for physical than for biological variables. This suggestion is also in agreement with the findings of Taylor *et al.* (2002), which have recently provided evidence for an amplification of climate signals by ecosystems. As a result, phytoplankton biomass,

C. finmarchicus, salmon and to a lesser extent, total copepods and euphausiids, have reached exceptionally low or high levels of abundance. This unusual period corresponds with anomalous positive values in NHT anomalies, SST and in the winter NAO index. However, the reversal seen in this latter index of climatological

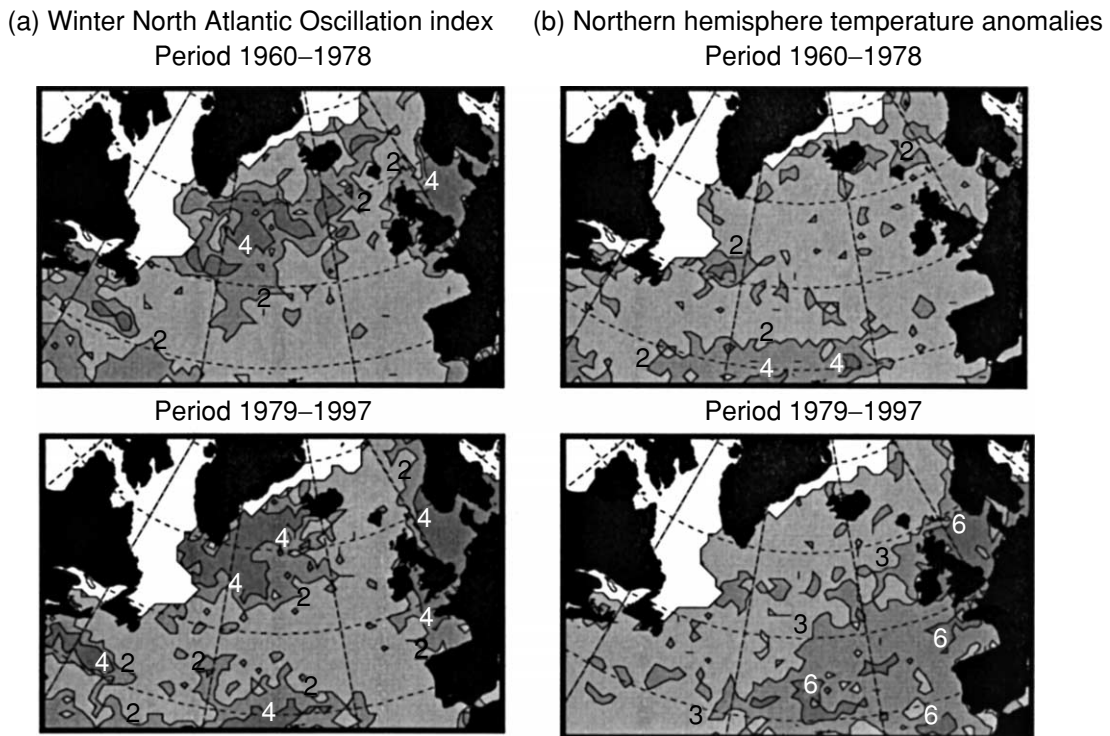


Fig. 10 Relationships between (a) the NAO and SST and (b) NHT anomalies and SST for 1960–1978 and 1979–1997. Maps indicate the number of months per pixel for which the probability of correlations between monthly sea surface temperature and the winter NAO index (a) and monthly NHT anomalies (b) was inferior to 10%. Probabilities were corrected to account for temporal autocorrelation. See Materials and methods.

variability after 1995 is not matched by the biology, which has remained anomalous for *C. finmarchicus*, a result also found by Planque & Reid (1998).

Phytoplankton colour has been shown to have increased substantially in the North Sea and in an area west of the British Isles after the mid-1980s, whereas the pattern of change was the reverse in the eastern Atlantic to the north of 59°N south of Iceland (Reid *et al.*, 1998; Edwards *et al.*, 2001). This pattern changed after 1996 north of 59°N with a strong increase in phytoplankton colour. This result corresponds well with the increased flow in the Irminger Current to the west of Iceland bringing in warm water. This study confirmed the patterns of long-term changes in phytoplankton colour detected by Reid *et al.* (1998) and the reversal seen south of Iceland (Reid & Beaugrand, 2002). The new higher levels of colour have been maintained in the North Sea. A number of other terrestrial or marine studies have also reached similar conclusions and have attributed this increase in phytoplankton or plant biomass to rising temperature (Keeling *et al.*, 1996; Myneni *et al.*, 1997; Reid *et al.*, 1998; Sturm *et al.*, 2001) although the increase in atmospheric CO₂ concentration may also play a role (Hein & Sand-Jensen, 1997; Ladeau & Clark, 2001).

The total number of copepods (inferior to 2 mm) was used as a measure of zooplankton abundance (secondary production). It has been previously used by Taylor & Stephens (1980), Hays *et al.* (1993) and Taylor (1995) to investigate relationships between copepods and the Gulf Stream North Wall index. Biogeographical studies indicate an increase in the mean body size northwards (Angel, 1998; Longhurst, 1998; Beaugrand unpublished data). Thus, this increase in the abundance of small copepods, in association with the decrease in the abundance of the cold-water species *C. finmarchicus* and euphausiids are in agreement with modifications expected with temperature increase. Recently, large-scale changes in the biogeography of calanoid copepod crustaceans have been described for the northeastern North Atlantic Ocean and adjacent seas. Strong biogeographical shifts in all copepod assemblages have been detected with a northward extension of more than 10° in latitude of warm-water species associated with a decrease in the number of colder-water species (Beaugrand *et al.*, 2002). Other studies have also shown a northward extension of the ranges of many warm-water fish (Quero *et al.*, 1998; Stebbing *et al.*, 2002). This evidence, combined with the present study tends to indicate a shift of marine pelagic

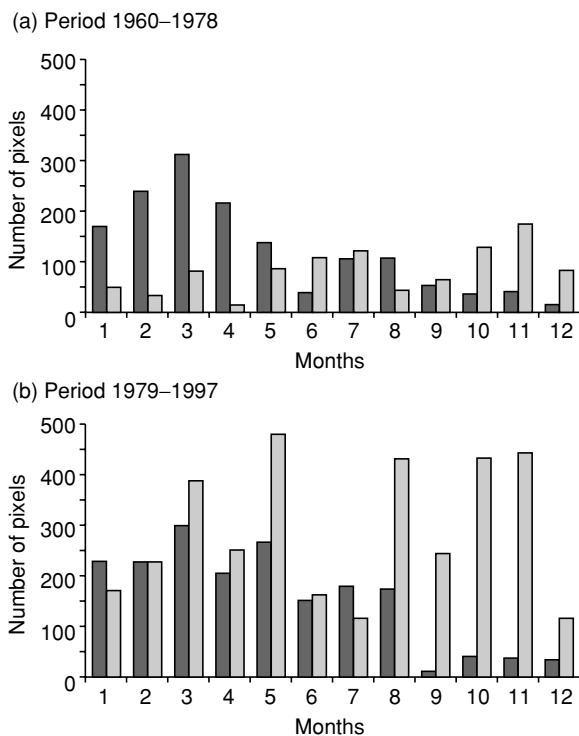


Fig. 11 Number of pixels which have a significant relationship ($P < 0.10$ after correction to account for temporal autocorrelation) between the winter NAO index and monthly sea surface temperature (dark grey) and between monthly NHT anomalies monthly sea surface temperature (slight grey) and for the period 1960–1978 (a) and 1979–1997 (b).

ecosystems towards a warmer dynamic regime in the northeastern North Atlantic. In terrestrial ecosystems in west Europe, similar changes in spatial distribution and phenology have been detected for many species of plants (Myneni *et al.*, 1997; Fitter & Fitter, 2002), butterflies (Parmesan *et al.*, 1999), amphibians (Beebee, 1995) and birds (Thomas & Lennon, 1999) and attributed to climatic change.

Analyses of hydro-climatic parameters have shown that the spatial pattern of correlations between the NAO and SST remained approximately stable before and after 1978. It indicates that the winter NAO index has a positive influence on SST especially in the North Sea while its influence is negative in the subarctic gyre. This pattern agrees with that of Hurrell & van Loon (1997) and Dickson & Turrell (2000). The influence of the NAO on SST was reinforced in spring after 1978. In contrast to the NAO, the spatial pattern of correlation between NHT anomalies and SST has radically changed after 1978. NHT anomalies have now a significant positive influence on SST in the northeast Atlantic from autumn to spring months (Figs 9 and 10), a result also found by Beaugrand *et al.* (2002). This study and the present one provide

evidence that NHT anomalies and SST positively covary in the northeast Atlantic. It is likely that the low-frequency variability in the NAO and high positive NHT anomalies have conspired together to produce the exceptional period detected after 1986. It is still an open debate if there is a relationship between the recent positive trend in the NAO and rising temperature (Hurrell *et al.*, 2001). Our study indicates a possible positive link at least when the 8-year cyclical variability of both climatological parameters is considered. Although difficult to detect, it seems likely that greenhouse-induced rising temperature in the Northern Hemisphere has influenced the positive trend in the North Atlantic Oscillation (Paeth *et al.*, 1999). Using the coupled atmosphere-ocean general circulation model ECHAM-3/LSG forced by an increased CO₂ concentration (IPCC Scenario A, Intergovernmental Panel on Climate Change, 2001), these authors found statistical evidence that the increase in atmospheric CO₂ concentration had a significant impact on the variability of the NAO. The difference in timing observed between the influence of the NAO (winter and spring) and NHT anomalies (autumn to spring) in this study suggest that these two factors may influence in different ways physical and biological processes. It is therefore important to investigate in the future long-term changes in the phenology of marine planktonic species, which could lead to the distinction between both types of hydro-meteorological forcing.

Conclusions

Climate change therefore appears to be an important parameter that is at present governing the dynamic equilibrium of pelagic ecosystems in the northeast Atlantic. If the increase in Northern Hemisphere temperature predicted by the Intergovernmental Panel on Climate Change (2001) continues, a marked change in the organisation of pelagic ecosystems from phytoplankton to fish can be expected with a possible impact on biogeochemical cycles, especially carbon sequestration by the ocean. It is expected that the decline in the abundance of salmon returning to homewaters will continue, particularly at the southern limit of their spatial distribution (Spain and France). Our results also open the way for the development of predictive tools, based on physical and plankton indicators, that could be used to assess future changes in the abundance and distribution of salmon returning to homewaters.

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