

# The North Sea regime shift: evidence, causes, mechanisms and consequences

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## Abstract

This paper focuses on the ecosystem regime shift in the North Sea that occurred during the period 1982–1988. The evidence for the change is seen from individual species to key ecosystem parameters such as diversity and from phytoplankton to fish. Although many biological/ecosystem parameters and individual species exhibited a stepwise change during the period 1983–1988, some indicators show no evidence of change. The cause of the regime shift is likely to be related to pronounced changes in large-scale hydro-meteorological forcing. This involved activating of complex intermediate physical mechanisms which explains why the exact timing of the shift can vary from 1982 to 1988 (centred around two periods: 1982–1985 and 1987–1988) according to the species or taxonomic group. Increased sea surface temperature and possibly change in wind intensity and direction at the end of the 1970s in the west European basin triggered a change in the location of an oceanic biogeographical boundary along the European continental shelf. This affected both the stable and substrate biotope components of North Sea marine ecosystems (i.e. components related to the water masses and components which are geographically stable) circa 1984. Large-scale hydro-climatic forcing also modified local hydro-meteorological parameters around the North Sea after 1987 affecting the stable biotope components of North Sea ecosystems. Problems related to the detection and quantification of an ecosystem regime shift are discussed.

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## 1. Introduction

The term ‘regime shift’ has been used to describe large, decadal-scale switches in the abundance and composition of plankton and fish (Reid, Borges, & Svendsen, 2001a). This term means a ‘catastrophic shift’ (abrupt shift) from one dynamic regime to another (Scheffer, Carpenter, Foley, Folke, & Walker, 2001a). Such an event is thought to have taken place in the northern part of the Pacific Ocean during the mid-1970s. Venrick, McGowan, Cayan, and Hayward (1987) reported an increase in phytoplankton biomass before and after this period, which they attributed to a modification of atmospheric circulation. Spatial gradients in sea level pressure increased the shift. Increased strength and frequency of storminess and west winds allowed a deeper mixing and a transfer of more nutrients to the surface. This climatic forcing modified the carrying capacity of the central North Pacific gyre, contributing to an increase in the abundance of fishes such as the Alaskan salmon and cod and a decrease in the abundance of shrimps (Botsford, Castilla, & Peterson, 1997). More recently, Reid et al. (2001a) suggested that a similar shift occurred in the North Sea after 1987. It involved an increase in phytoplankton biomass (Reid, Edwards, Hunt, & Warner, 1998), a change in zooplankton community structure and organism phenology (Beaugrand & Reid, 2003; Reid et al., 2001a) and was also detected in the benthic realm (Reid & Edwards, 2001).

It has been difficult to demonstrate shifts between alternative stable dynamic regimes in the real world (Scheffer et al., 2001a). To demonstrate that an ecosystem regime shift may have actually happened (in a

pelagic ecosystem), stepwise changes should be detected (1) across different trophic levels, (2) at the level of the community structure, (3) for key species, (4) in attributes of ecosystems such as diversity and (5) one should expect that ecosystem changes would reflect hydro-climatic variability.

I focus here on the ecosystem regime shift in the North Sea. The objectives of this paper are to (1) provide evidence that stepwise changes occurred across trophic levels, at the level of the community (e.g. calanoid copepods) and in some key attributes of pelagic ecosystems in the north-east Atlantic and in the North Sea and to (2) propose an explanation of what could be the causes of the shift. Evidence for and against the North Sea regime shift are presented and the discussion considers conceptual and methodological problems involved in the detection of regime shifts in marine pelagic ecosystems.

## 2. Materials and methods

### 2.1. Biological data

Biological data used in this study were collected by the continuous plankton recorder (CPR) survey. The CPR is an upper layer plankton monitoring programme that has been operated on a routine monthly basis in the North Atlantic and North Sea since 1946 (Warner & Hays, 1994). Sampling is carried out by a high-speed plankton recorder (about 20 km h<sup>-1</sup>) that is towed behind voluntary merchant ships at a standard depth of approximately 6.5 m. One CPR sample corresponds to about 3 m<sup>3</sup> of seawater filtered (Warner & Hays, 1994). Only data corresponding to the period 1958–1999 were used to investigate the long-term changes in the spatial distribution of species associations.

Total calanoid copepod biomass per CPR sample was estimated from the size of each calanoid copepod (a total of 108 possible species of calanoids), their abundance and allometric relationships (Peters, 1983). The mean size of calanoid copepod (minimum size of female) per CPR sample was also calculated. Adult females or copepodite stage V were chosen because they represent the majority of copepods caught in the samples (Mauchline, 1998).

Data on fish recruitment were derived from virtual population analysis and are from ICES (2001). Five species (Plaice: *Pleuronectes platessa*, cod: *Gadus morhua*, haddock: *Melanogrammus aeglefinus*, herring: *Clupea harengus*, sole: *Solea solea*) were used in the study.

### 2.2. Physical data

Both temperature and salinity (bottom and surface), ICES data for the North Sea, were provided by Keith Brander (ICES, Copenhagen). A programme was written to calculate the annual mean of each ICES variable in the four areas selected in the North Sea.

COADS (comprehensive ocean-atmosphere data set) 1-degree enhanced data were provided by the NOAA-CIRES Climate Diagnostics Center (Boulder, CO, USA; Woodruff, Slutz, Jenne, & Steurer, 1987). Both temperature and wind intensity (westerly wind intensity and northerly wind intensity) were used.

Surface temperature anomalies for the Northern Hemisphere (NHT) from 1958 to 1999 were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, London, UK.

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 between the Subtropical and the Arctic Atlantic (Hurrell, 1995). The index used here is based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864 (Hurrell, 1995).

### 2.3. Statistical analyses

Three different techniques were applied to identify and quantify the regime shift using the CPR phytoplankton colour index, total biomass of calanoid copepods per CPR sample and an index of calanoid copepod diversity (as the mean number of calanoid species per CPR sample). For each biological parameter, the value for each month from 1958 to 1999 was considered.

#### 2.3.1. Split moving-window boundary analysis

Split moving-window boundary analysis (SMW, Webster, 1973) was used to identify temporal discontinuities in the multivariate time series (12 months  $\times$  42 years). This method has been recently applied by Beaugrand (2003). It allows (1) detection of discontinuities that can be related to regime shifts and (2) the quantification of observed changes by the calculation of a probability level. The calculation of SMW is realised in four steps. (1) A window of even-numbered size is introduced at the beginning of the time series (here, a window of 10 years was selected; Beaugrand, 2003). (2) This window is then divided into two half-windows. (3) An association coefficient (here, the Euclidean distance) is used to evaluate the differences between those time periods. A multiple response permutation procedure (MRPP; Mielke, Berry, & Brier, 1981) was applied to test the two periods on the basis on the information provided by all months. (4) The window is then moved from year to year, repeating steps 2 and 3 until the end of the time series is reached.

#### 2.3.2. Principal component analysis

A standardised principal component analysis (PCA) was applied to the table of 12 months  $\times$  42 years.

#### 2.3.3. Cluster analysis

A hierarchical flexible agglomerative clustering method (Lance & Williams, 1967) was performed on data smoothed to decrease the influence of episodic events or other high-frequency variability. The smoothing was realised by a singular spectrum analysis (Vautard, Yiou, & Ghil, 1992), also called eigenvector filtering (Ibañez & Etienne, 1991). Original data (a of table 12 months  $\times$  42 years) were recalculated from the first two eigenvectors and principal components. The Euclidean distance was then used to calculate the distance matrix, 42 years  $\times$  42 years. Probabilities of significance between periods detected by the cluster analysis were then calculated using the MRPP test on the original unsmoothed data.

Long-term changes (1964–1999) in fish recruitment (five species) were investigated by the use of a standardised PCA. Another standardised PCA was performed on five hydro-climatic parameters (sea surface temperature, westerly wind, northerly wind, North Atlantic Oscillation, Northern Hemisphere Temperature anomalies) for the period 1960–1997 to reveal long-term changes in hydro-climatic forcing. All methods were programmed in the MATLAB language.

## 3. Evidence for an ecosystem regime shift in the North Sea

Reid et al. (2001a) were the first to suggest that a regime shift may have happened in the North Sea. Using biological indicators, they showed that the North Sea pelagic ecosystem underwent dramatic changes observed from phytoplankton to fish after the mid-1980s. Reid and Edwards (2001), using data from Kroncke (personal communication), provided evidence that these changes may have also happened in the benthos. However, the existence of a regime shift in the North Sea is still debated (Reid & Beaugrand, 2002; Taylor, 2002). This section reviews evidence for and against the ecosystem regime shift in the North Sea but also draws attention to some conceptual and methodological problems in detecting and quantifying regime shifts in marine ecosystems.

### 3.1. Phytoplankton

More than one hundred phytoplankton species or groups have been recognised since the beginning of the CPR survey. However, changes through time have only been examined for a few groups (e.g. Edwards, Reid, & Planque, 2001). Research has focussed mainly on phytoplankton colour, an index thought to reflect phytoplankton biomass (Reid et al., 1998). Examination of this index has typically shown a pronounced increase in the north-east Atlantic and in the North Sea after the mid 1980s (Beaugrand & Reid, 2003; Reid et al., 2001a). Figs. 1(a)–(b) present long-term monthly changes of this index. Using the Webster/MRPP methods, two significant discontinuities were detected in this data. The first occurred after 1972–1973 and the second after 1985–1986 (Fig. 1(c)). It should be noted that this procedure showed both discontinuities at

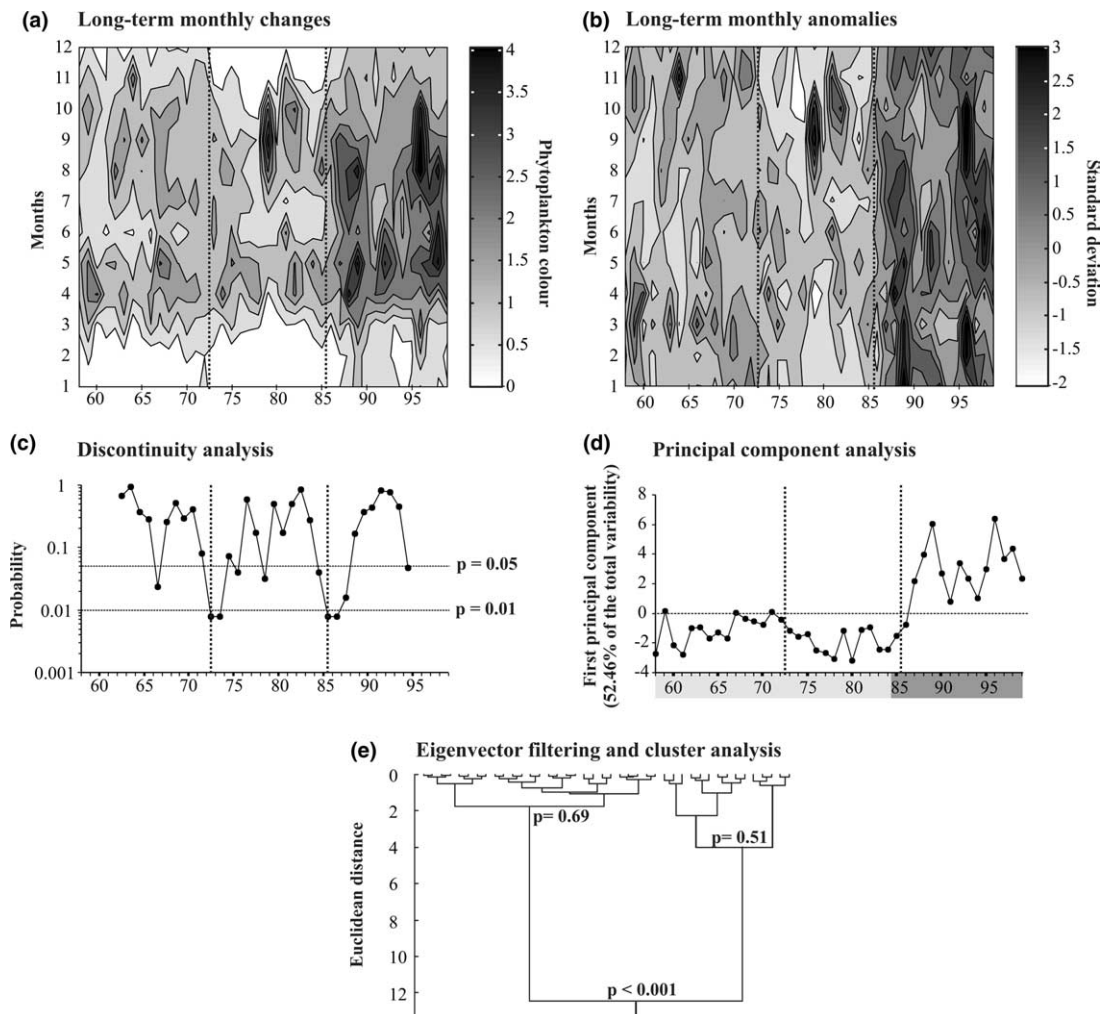


Fig. 1. Long-term changes in phytoplankton colour in the North Sea. (a) Long-term monthly changes in phytoplankton colour. (b) Long-term monthly anomalies in phytoplankton colour. (c) Results of the SMW/MRPP procedure. Horizontal dashed lines indicate probability level of 0.01 and 0.05. (d) First principal component (52.46% of the total variability) from a standardised PCA applied to the matrix 12 months  $\times$  42 years. Vertical dashed lines on (a)–(d) indicate the period of the shift. (e) Cluster analysis. Probabilities of significance between periods detected by the cluster analysis are indicated.

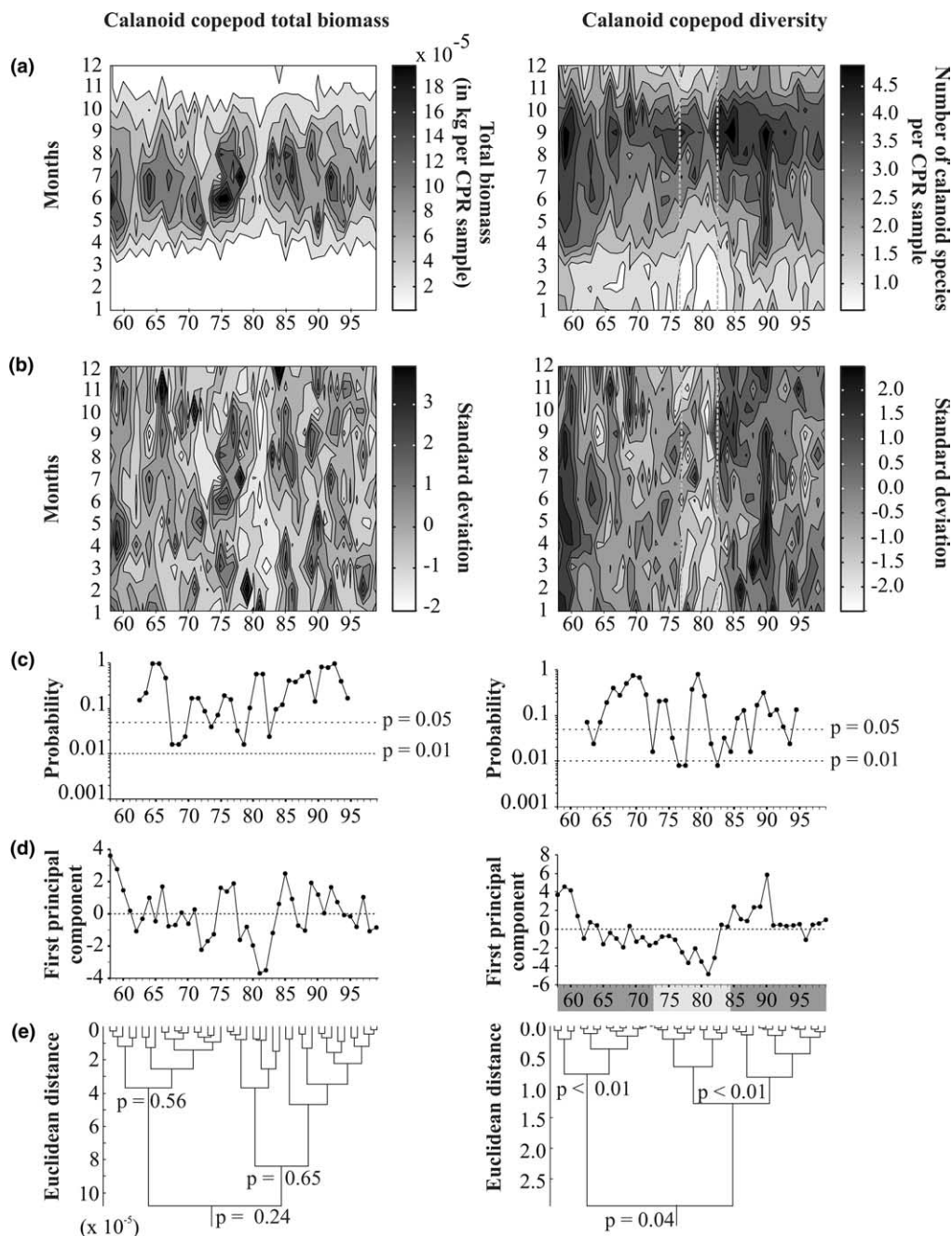


Fig. 2. Long-term changes in calanoid copepod biomass (left) and diversity (right) in the North Sea. (a) Long-term monthly changes in calanoid copepod biomass (left) and diversity (right). (b) Long-term monthly anomalies in calanoid copepod biomass (left) and diversity (right). (c) Results of the SMW/MRPP procedure for calanoid copepod biomass (left) and diversity (right). Horizontal dashed lines indicate probability level of 0.01 and 0.05. (d) First principal components (20.87% of the total variability for biomass at the left and 40.79% of the total variability for diversity at the right) from a standardised PCA applied to the matrix 12 months  $\times$  42 years. Vertical dashed lines on Fig. 1(a)–(d) (right only) indicate the period of the shift. (e) Cluster analysis. Probabilities of significance between periods detected by the cluster analysis are indicated.

the same level of significance, although a visual examination indicates that the change after 1985–1986 is more pronounced (Figs. 1(a)–(b)). This latter observation is reinforced by the results of a standardised PCA (Fig. 1(d)) and a cluster analysis, which both emphasise the exceptional character of the change that took place in the colour after the mid-1980s.

It is the combination of the three techniques that allowed a good identification of the stepwise changes and the characterisation of the different periods in the phytoplankton colour time series. It has been recently suggested that the colour shift should also reflect changes in phytoplankton community structure (Martin Edwards, personal communication). Future studies should also focus on phytoplankton species and examine whether the stepwise changes seen in the phytoplankton colour index do reflect changes in phytoplankton community structure.

### 3.2. Zooplankton

Zooplankton have been investigated in greater detail than phytoplankton (e.g. Beaugrand, Ibañez, & Lindley, 2003; Beaugrand & Reid, 2003; Reid & Edwards, 2001). Studies have focused on individual zooplankton species using multivariate analyses (e.g. Beaugrand et al., 2003; Reid & Edwards, 2001) and more recently on diversity and species assemblage indicators (Beaugrand, 2003; Beaugrand & Ibañez, unpublished data). This section covers long-term changes in zooplankton from individual species to the whole community structure, using key properties of the ecosystems such as biomass and diversity.

### 3.3. Calanoid copepod biomass and diversity

Figs. 2(a)–(b) show long-term monthly changes in total biomass and diversity (as the number of calanoid copepod species per CPR sample) of calanoids in the North Sea. No clear pattern of variability was evident for total biomass, while three periods can be visually identified for calanoid diversity. This is confirmed by the discontinuity analysis, which detected no significant stepwise change (at a threshold of 1%) for biomass and two discontinuities (1: 1976–1977 and 2: 1982) for diversity (Fig. 2(c)). The first principal component (20.87% of the total variability) of the PCA performed on biomass data emphasised a period of low biomass during the cold-biological episodic event (Edwards, Beaugrand, Reid, Rowden, & Jones, 2002; Edwards et al., 2001). This exceptional event occurred during the period 1978–1982 and was characterised by a strong decrease in the number or biomass of many taxonomic groups, such as dinoflagellates, diatoms and

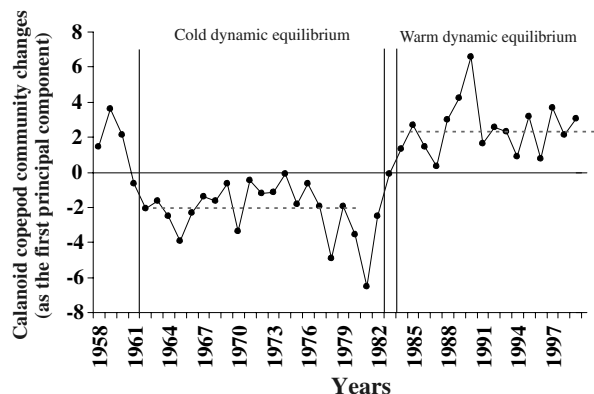


Fig. 3. Long-term changes (1958–1999) in the first principal component (32.46% of the total variability). A PCA was performed on the Beaugrand et al. (2002a) species assemblage indicators in four regions of the North Sea (a total of 23 indicators representing all components of the calanoid copepod community structure). From Beaugrand and Ibañez (unpublished data).

decapods (Edwards et al., 2002). Increases in species indicative of cold water intrusion were also detected (Beaugrand, in press; Edwards et al., 2002).

The first principal component (40.79% of the total variability) of the PCA performed on diversity data shows a period (about 1978–1982) of low diversity during the cold-biological episodic event, followed by a period of sustained high diversity (Fig. 2(d)). The cluster analysis did not identify any significant period (MRPP tests not significant) for biomass, while the analysis of diversity data found three periods (Fig. 2(e)). It should be noted that the limits between periods identified by the cluster analysis (1972 and 1984) do not correspond to the two discontinuities (1: 1976–1977 and 2: 1982) found by the Webster/MRPP tests. This substantial difference indicates that the timing of a shift should be considered as approximate. This difference can be explained by the smoothing done by the eigenvector filtering method (i.e. moving average weighted by the eigenvectors) prior to the cluster analysis. It is likely that the smoothing makes the detection of the boundary between the periods more difficult.

### 3.4. Calanoid copepod community structure

Recently, calanoid copepods have been divided into species assemblages (Beaugrand, Ibañez, Lindley, & Reid, 2002a). Beaugrand (in press) proposed the use of these species assemblages as indicators to monitor

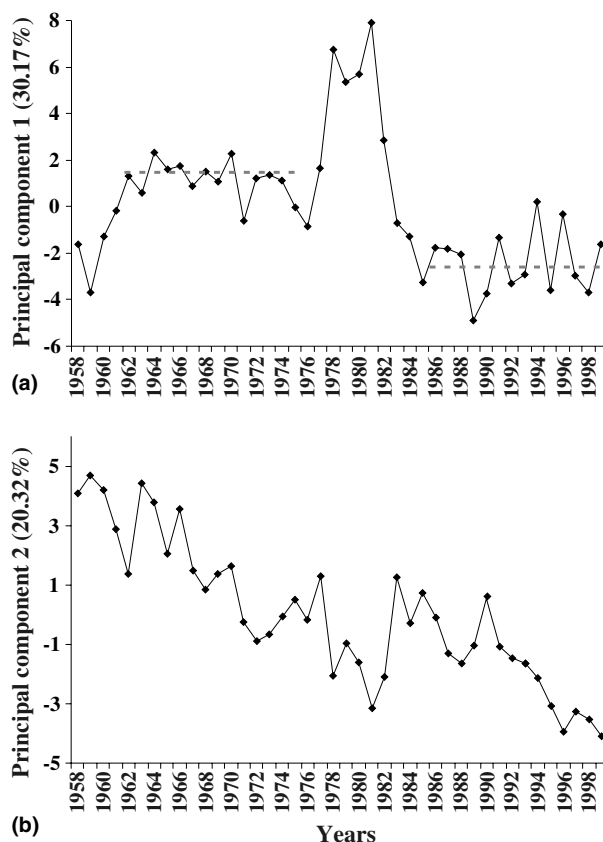


Fig. 4. (a) First principal component (30.17% of the total variability) from a standardised PCA performed on the abundance (1958–1999) of the 28 most abundant zooplankton taxa or species in the North Sea. Horizontal grey dashed lines emphasise periods of dynamic equilibrium. (b) Second principal component (20.32% of the total variability). From Beaugrand et al. (2003).



the responses of pelagic plankton ecosystems to climate change. Beaugrand and Ibañez (unpublished data) applied these species assemblage indicators and identified pronounced changes at the scale of the community after the beginning of the 1980s (Fig. 3). The period prior to the shift (1962–1982) was called a ‘cold dynamic equilibrium’ (e.g. high abundance of species indicative of a cold environment, low calanoid diversity) while the period after the shift (1984–1999) was called a ‘warm dynamic equilibrium’ (e.g. low abundance of species indicative of a warm environment, high calanoid diversity). Although some species

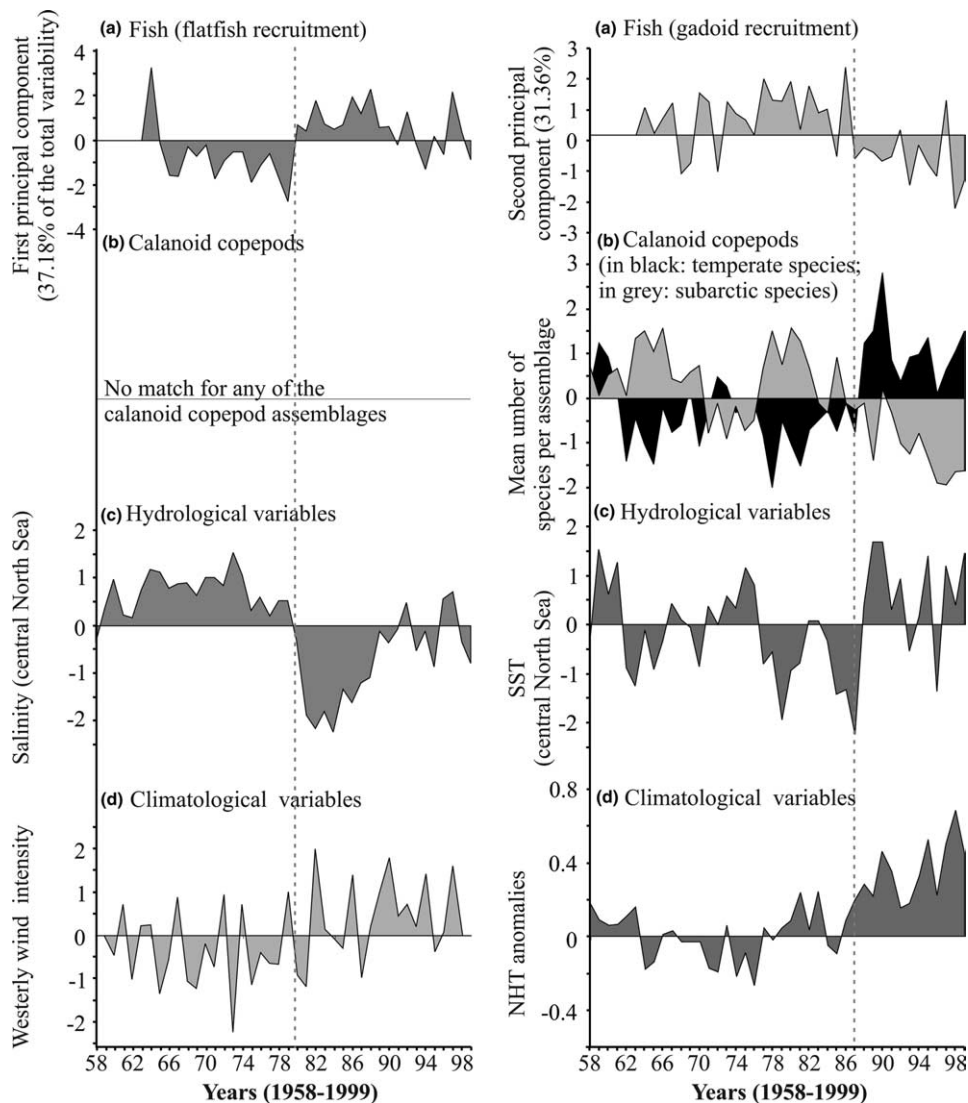


Fig. 5. Long-term changes in fish abundance in relation to year-to-year changes in calanoid copepod composition and hydro-meteorological forcing. (a) Long-term changes in fish recruitment (herring, cod, haddock, plaice, sole). On the left side, the first principal component (37.18% of the total variability) is mainly represented by the flatfish plaice and sole. On the right side, the second principal component (31.36% of the total variability) is mainly represented by the gadoid species haddock and cod. (b) Long-term changes in calanoid copepod species composition. No match was found between changes in calanoid and flatfish. (c) Changes in hydrological variables (salinity on the left side and sea surface temperature on the right side). (d) Changes in meteorological forcing (westerly wind intensity over the North Sea on the left side and Northern Hemisphere Temperature anomalies on the right side).

assemblages, especially in the southern part of the North Sea, did not show clear evidence of a stepwise change, nearly all species assemblages showed a pronounced shift in the central and northern part of the North Sea after the beginning of the 1980s.

### 3.5. Other zooplankton species

Beaugrand et al. (2003) analysed the 28 most abundant zooplankton species in the North Sea and found a pronounced change after the beginning of the 1980s, in addition to the clear detection of the cold-biological episodic event (Fig. 4(a)). Results were similar to those found for calanoid copepod species. The period after the beginning of the 1980s was characterised by a decrease in some taxa or species, such as *Calanus finmarchicus* and euphausiids, and increases in taxa such as decapods, echinoderm and lamelli-branch larvae, *Podon* and *Evadne* (Edwards et al., 2002). Only a few species (e.g. *Limacina retroversa* and *Oithona* spp.) did not show any evidence of a shift but instead a more or less continued decrease in abundance (Fig. 4(b)).

### 3.6. Fish

A standardised PCA extracted the main pattern of long-term variability in fish recruitment (five species of fish: plaice, sole, herring, haddock, cod) during the period 1964–1999 (Fig. 5(a), left). The first principal component (37.18% of the total variability) showed a stepwise change in 1980 prior to the regime shift (between 1983 and 1989). Changes in the first principal component were related to flatfish (positive correlation with the first principal component). This indicates that an increase in the first principal component reflects an increase in flatfish recruitment. The timing of this change was not matched by any of the changes in calanoid copepod assemblages (Fig. 5(b), left), but was linked to salinity changes in the of the North Sea (Fig. 5(c), left). The fluctuations observed were only partially matched by changes in the intensity of westerly wind (Fig. 5(d)). For these indicators, no shift was detected.

Long-term changes in gadoid species were positively correlated to the second principal component (31.36% of the total variability, Fig. 5(a) right). Fluctuations in this principal component did parallel changes in calanoid copepod composition and sea surface temperature (Figs. 5(b)–(c), right). The right panel of Fig. 5 clearly shows the exceptional character of the period after 1987, which corresponded with strong positive Northern Hemisphere Temperature anomalies and a prolonged period of positive NAO. Gadoid recruitment shows a pronounced change after 1987.

## 4. Evidence for a climatological regime shift in the north-east Atlantic

Oceanographers have long recognised the importance of changes in weather and physical oceanographic conditions in the modification of pelagic ecosystems (e.g. Colebrook, 1985; Hardy, 1939; Russell, 1939). Therefore, it can be expected that the ecosystem regime shift in the North Sea paralleled a stepwise shift in climate. The previous section has shown that most biological/ecosystem indicators have exhibited pronounced changes between 1983 and 1987 (Table 1). When indicators are taken individually, the timing of the shift can vary greatly within the 5-year period (see also Beaugrand & Reid, 2003; Beaugrand and Ibañez, unpublished data) but is centred around two periods: 1984–1985 and 1987–1988. The latter shift, 1987–1988, is matched by a pronounced change in climate. A principal component analysis was performed using five hydro-climatic parameters: sea surface temperature, westerly wind intensity, northerly wind intensity (averaged for the whole North Sea) and North Atlantic Oscillation and Northern Hemisphere Temperature anomaly. The first principal component shows a pronounced change after 1987. This result (see also Beaugrand, 2003) demonstrates that the stepwise changes in some biological/ecosystem indicators

Table 1

Biological/ecosystem indicators and methods used to test the hypothesis of a regime shift in the North Sea

Biological/ecosystem indicators	Timing of change	Methods	Authors or figures from this study
CPR phytoplankton colour	1988	Visual examination of graphics	Reid et al. (2001a, 2001b)
Abundance of horse mackerel ( <i>Trachurus trachurus</i> )			Reid and Edwards (2001)
Zooplankton principal component (based on 24 species)			Reid and Beaugrand (2002)
Benthic biomass (Kröncke data)			Reid, Edwards, Beaugrand, Skogen, and Stevens (2003)
Abundance of <i>C. finmarchicus</i>			
Abundance of <i>C. helgolandicus</i>			
Other species or taxonomic groups were examined but results were not shown			
SSB cod ( <i>Gadus morhua</i> )	No shift	Vector autoregressive process and Bootstrap	Solow and Beet (in press)
SSB haddock ( <i>Melanogrammus aeglefinus</i> )			
SSB herring ( <i>Clupea harengus</i> )			
CPR phytoplankton colour			
Category 'total copepods' (averaged for the whole North Sea)			
CPR 'total copepods' category (averaged for the whole North Sea)	No shift	Cumulative sums	Taylor (2002)
Abundance of <i>C. finmarchicus</i>			Beaugrand and Reid (2003)
Abundance of <i>C. helgolandicus</i>			Beaugrand and Reid (2003)
CPR phytoplankton colour (long-term monthly changes)	1985–1986	SMW/MRPP/Cluster analysis/PCA	Fig. 1
CPR phytoplankton colour (long-term annual changes)	1985		Beaugrand and Reid (2003)
Category 'total copepods' (North-east North Sea)	1984		Beaugrand and Reid (2003)
Total calanoid copepod biomass	No shift		Fig. 2
Abundance of euphausiids	1982		Beaugrand (2003)
Abundance of Atlantic salmon ( <i>Salmo salar</i> )	1988		Beaugrand and Reid (2003)
Abundance of <i>C. finmarchicus</i> (long-term annual changes)	1985		Beaugrand and Reid (2003)
Abundance of <i>C. finmarchicus</i> (long-term monthly changes)	1985–1986		Beaugrand and Reid (2003)
Abundance of <i>C. helgolandicus</i> (long-term monthly changes)	1981–1984, 1987–1988		Beaugrand (2003)
Zooplankton PC1 (analysis based on 28 species or taxonomic groups)	1985		Beaugrand and Reid (2003)
Species assemblage indicators PC1 (analysis based on 23 species assemblages in four regions of the North Sea)	1983		Fig. 4
Calanoid copepod diversity (long-term monthly changes)	1982–1984		Fig. 2
Gadoid recruitment	1987		Fig. 5
Flatfish recruitment	No shift		Fig. 5

SSB: spawning stock biomass. PC1: first principal component.

(see Table 1) are matched by a pronounced (statistically significant) change in hydro-meteorological forcing (sea surface temperature in the North Sea and for wind intensity) in the North Sea. Yasunaka and Hanawa (2002) also found a regime shift in the Northern Hemisphere sea surface temperature field (during wintertime) in 1988/1989. A significant change was also noted in large-scale climatological variables such as the

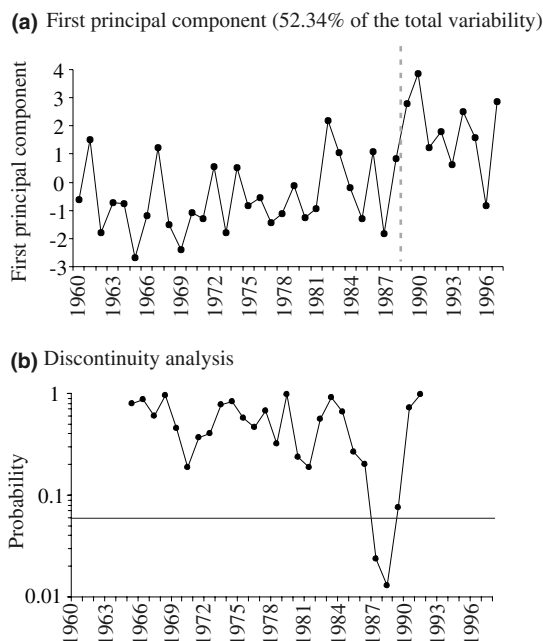


Fig. 6. (a) Long-term changes (1960–1997) in the first principal component (52.34% of the total variability) from a PCA performed on five hydro-climatic parameters. The vertical dashed grey line indicates the time of the first significant discontinuity. (b) Results of SMW/MRPP indicating the timing of the discontinuities in the multivariable hydro-climatic time series.

North Atlantic Oscillation and Northern Hemisphere Temperature anomalies by Beaugrand and Reid (2003) and Beaugrand (2003). These results, therefore, indicate a causative mechanism for the ecosystem regime shift. The change seems more difficult to detect in physical than in biological time series, which may indicate that biological processes amplify environmental signals, an hypothesis recently suggested by Taylor, Allen, and Clark (2002). Studying the impact of regime shifts on food webs in shallow lakes, Scheffer, Straile, van Nes, and Hosper (2001b) also concluded that small climatic changes may trigger major regime shifts in ecosystems (see Fig. 6).

## 5. Hypotheses proposed to explain the regime shift in the North Sea

It has been hypothesised that the regime shift in the North Sea resulted from the conjunction of three main features: (1) a change in local hydro-meteorological forcing (Beaugrand, 2003; Beaugrand & Reid, 2003; Reid et al., 2001a); (2) a displacement of oceanic biogeographical boundaries to the west of the European continental shelf (Beaugrand, 2003); and (3) an increase in oceanic inflow into the North Sea (Reid et al., 2001a, 2001b; Reid et al., 2003). These features are linked with each other and it is proposed that they have been influenced by common and large-scale climatological forcing. Fig. 7 summarises the different factors/processes involved in the regime shift.

### 5.1. Change in local hydro-meteorological forcing after 1987

The previous chapter provided evidence that the regime shift in the North Sea ecosystem paralleled a pronounced change in some regional hydro-climatic parameters (wind intensity and sea surface temperature) after 1987 (see Fig. 5). Changes in these physical parameters in the North Sea have been strongly

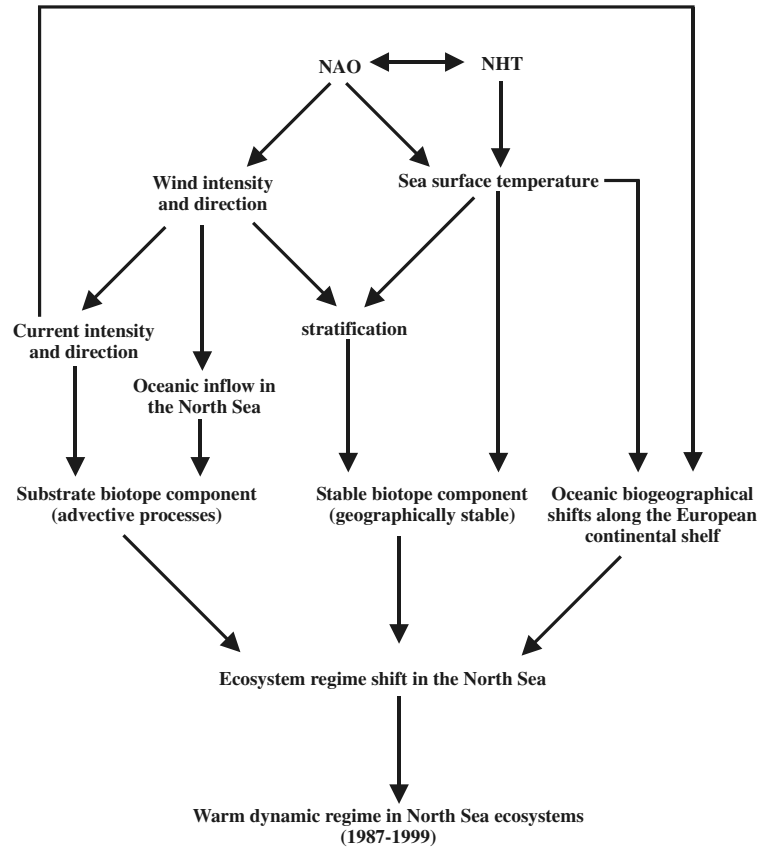


Fig. 7. Factors and processes thought to be involved in the North Sea ecosystem regime shift.

related to the North Atlantic Oscillation (Dickson & Turrell, 2000; Reid & Planque, 2000), which also shows significant stepwise changes after 1987 (Beaugrand, 2003; Beaugrand & Reid, 2003). The increase in regional sea temperature has triggered a change in calanoid copepod species composition and diversity (Beaugrand & Ibañez, 2002; Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002c). Generally, warm-water species have increased, while colder-water species have decreased in the North Sea (see Fig. 5). An increase in both phytoplankton and zooplankton species considered as indicative of stratified water has also been reported (Edwards et al., 2002) although the average of wind intensity seems to have increased over the North Sea (Beaugrand, 2003).

### 5.2. A displacement of oceanic biogeographical boundaries to the west of the European continental shelf (impact in the North Sea after 1982)

A change in local hydro-meteorological forcing over the North Sea occurred after 1987. However, some biological indicators show a stepwise change prior to 1987 (e.g. diversity after 1982–1984, see Fig. 2, Table 1). This has led Beaugrand (2003) to hypothesise that in addition to the local atmospheric forcing that influenced the regime shift in the North Sea, the stepwise change in the dynamic regime of North Sea pelagic ecosystems was triggered by a major reorganisation in the biological composition of ecosystems in the north-east Atlantic since the beginning of the 1980s (Beaugrand, Reid, & Ibañez, 2002b; Beaugrand

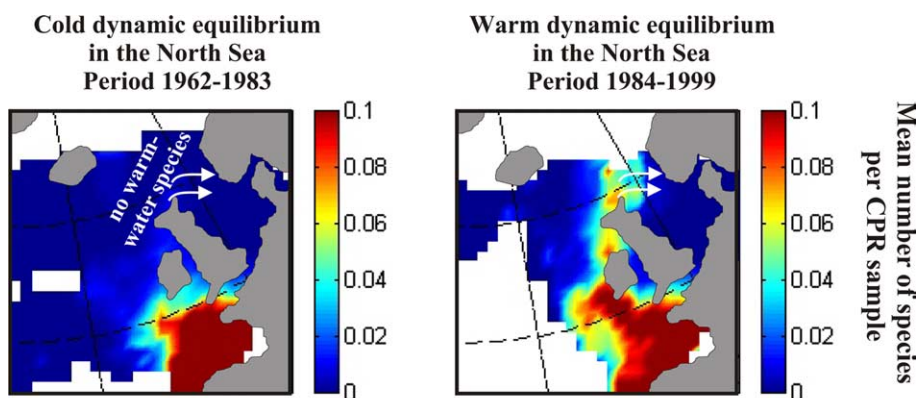


Fig. 8. Mean number of warm-temperate pseudo-oceanic species in the north-east Atlantic Ocean for the period 1962–1983 and 1984–1999. From Beaugrand and Ibañez (Unpublished data). The white arrow denotes oceanic inflow into the North Sea.

et al., 2002c). Along the European continental shelf, strong biogeographical shifts in all copepod assemblages have occurred, with a northward extension of warm-water species ranges by more than  $10^\circ$  in latitude, concurrent with a decrease in the number of colder-water species.

Fig. 8 shows the major change that happened for warm-temperate, pseudo-oceanic (i.e. species that can be seen in oceanic and neritic waters but occurring mainly above the shelf-edge) calanoid copepod species in the north-western part of the North Sea. The coincidence between the appearance of these assemblages in the North Sea and the shift in community structure after 1982 suggests a link between biogeographical changes in the north-east Atlantic and the regime shift in the North Sea. This result also suggests that the regime shift can be best understood if changes in diversity and community structure at the scale of, at least, the north-eastern North Atlantic are considered.

These biogeographical changes were correlated to sea surface warming the west-European basin, which showed a significant stepwise temperature increase at the end of the 1970s and 1980s (Beaugrand, 2003; Beaugrand et al., 2002c). The increase in the flow of the European shelf-edge current noted by Holliday and Reid (2001) and Reid, Holliday, and Smyth (2001b) could also have contributed to the biogeographical shift. Holliday and Reid (2001) investigated the transport of oceanic water into the Rockall Trough. They found that the mean volume transport reached about 7 sv in 1989 and 1998, nearly twice the usual rate (3.7 sv). These two periods of increase in the strength of the European shelf-edge current coincided with two episodic oceanographic events that occurred during the late 1980s and the late 1990s (warm biological episodic events; see Edwards, John, Hunt, & Lindley, 1999; Edwards et al., 2001). The latter event (late 1990s) was not clearly detected in the diversity and community structure of calanoid copepods. Subsequently, Reid et al. (2001b) provided indications that strong northward advection of warm water along the European shelf edge coincided with these two pulses of oceanic inflow into the North Sea.

### 5.3. Increase in oceanic inflow into the North Sea (after 1987)

Some authors have drawn attention to the importance of oceanic inflow for the ecology of the North Sea (Edwards et al., 1999; Lindley et al., 1990). Using the NORWECOM model (Skogen & Soiland, 1998). Reid et al. (2003) emphasised that modelled inflow to the North Sea was strongly related to the intensity of wind and the state of the North Atlantic Oscillation. The sustained positive phase of the North Atlantic Oscillation, having resulted in increased westerly wind intensity, has probably increased the volume of water advected into the North Sea. However, this process alone cannot explain why so many warm-water pseudo-

oceanic species have been detected after 1982 in the North Sea. As indicated by Fig. 8, in the case of strong oceanic inflow into the North Sea prior to 1982, no warm-water pseudo-oceanic species could have been advected into the North Sea. It is only after 1982 that a ‘seed’ pool of this species group is detected by the CPR survey in oceanic regions to the west of the North Sea. Therefore, changes in the biogeographic boundaries along the European continental shelf and advection of oceanic water into the North Sea have worked together in affecting the stepwise change observed in the North Sea in 1987. Local hydro-meteorological forcing has also played an important role, as shown by modifications in the benthos (Reid & Edwards, 2001) and meroplankton (see Section 3), combined with changes in local hydro-climatic forcing reported here.

## 6. Conceptual and methodological problems

The concept of a marine ecosystem regime shift suffers from a number of problems. The term itself sometimes has a different meaning among scientists (de Young et al., 2004). In climatology, Yasunaka and Hanawa (2002) defined a regime shift as “an abrupt transition from one quasi-steady climatic state to another, and its transition period is much shorter than the lengths of the individual epochs of each climatic state”. Operationally, Yasunaka and Hanawa (2002) defined regime shifts as “significant and systematic changes between two quasi-steady states, continuing more than 5 years”. Furthermore, all regime shifts (using Northern Hemisphere SST fields) detected in their study were completed within one year (Yasunaka & Hanawa, 2002). Although a one-year shift can be possible in physical data, it is perhaps too short for biological time series, which typically have a greater inertia (autocorrelation) than hydro-climatic time series. This study has shown that, according to the species or taxonomic group, the timing of the shift may change. Beaugrand and Reid (2003) stressed that difference in timing can be expected, since many species react differently to hydro-climatic forcing depending upon the particular threshold values of their physiological processes or their life history. The different spatial centre of distribution of species is also likely to explain this change in timing (see Table 1).

Some indicators showed evidence of a regime shift, while some did not (e.g. biomass and diversity in Fig. 2). These contrasting results between biomass and diversity may explain in part the current debate about the existence of a regime shift in the North Sea (e.g. Reid & Beaugrand, 2002; Taylor, 2002). In addition to the abundance of *Calanus finmarchicus* and *Calanus helgolandicus*, Taylor (2002) used the category ‘total copepods’. He was unable to find any evidence for a shift using this latter indicator. The categories ‘total copepods’ and calanoid copepod biomass are not good indicators of change. Their interpretation is not straightforward, as they can encompass a large number of species. Such indices may not detect changes in the community structure in some circumstances. For example, the total abundance of a taxonomic group can remain stable while the species composition changes. This situation occurred for *C. finmarchicus*, which has strongly decreased in the North Sea while its congener *C. helgolandicus* has increased (Beaugrand, 2003; Reid et al., 2003). Thus, these types of indicators may be less sensitive than key species indicators. Furthermore, this result may indicate that the regime shift in the North Sea involved more qualitative than quantitative changes. However, Taylor (2002) did not find any evidence for a regime shift using *C. finmarchicus* and *C. helgolandicus* while Beaugrand (2003) in contrast did find one.

The selection of biological/ecosystem parameters is crucial. If one wants to identify an ecosystem regime shift, ideally the analysis should cover organisms from viruses to picoplankton to nekton to seabirds, as well as abiotic parameters. This condition is rarely met and often only a restricted number of biological/ecosystem indicators has to be used. Commonly, four types of indicators have been used: (1) species indicators (e.g. Hare & Mantua, 2000); (2) indicators of primary and secondary production (e.g. Beaugrand & Reid, 2003; Reid et al., 2001a); (3) indicators of the dynamic regime of ecosystems (e.g. diversity indicators of a taxonomic group; Beaugrand et al., 2002a); and (4) species assemblage indicators (Beaugrand

et al., 2002c). For species with complex and long life histories such as gadoid fish, the correct parameter should be used. For example, using recruitment data for gadoids may more easily detect a shift than if spawning stock biomass is utilised, because this latter parameter has a greater inertia that may change the timing of the shift or mask its detection.

The statistical detection of an ecosystem regime shift is also a crucial point. Many statistical analyses can be used to identify, characterise and quantify a regime shift (Mantua, 2004). In the present study, time series analysis, ordination and cluster analysis were used. It has been shown by the analysis that the timing of a shift may change or be perceived differently depending on the statistics used. Furthermore, Rudnick and Davis (2003) have shown that a composite analysis (i.e. the procedure of Ebbesmeyer, Cayan, McLain, Nichols, Peterson, & Redmond (1991) used in Hare & Mantua, 2000) can lead to the identification of a spurious regime shift because of the red noise in the time series. A statistical procedure, applicable at the level of individual species, should be developed to better identify and quantify regime shifts. This procedure would probably overcome the problem emphasised by Rudnick and Davis (2003).

## 7. Conclusions

This study provides evidence that a regime shift occurred in the North Sea during the period 1982–1988 (centred around two periods: 1982–1985 and 1987–1988). It is seen from individual species (e.g. *C. finmarchicus*) to key ecosystem parameters such as diversity and from phytoplankton (CPR phytoplankton colour index) to zooplankton (holoplankton and meroplankton) to fish (Gadoid species). Although it is demonstrated that many biological/ecosystem parameters and individual species exhibited a stepwise change during the period 1982–1988, some indicators (e.g. total biomass of calanoid copepod) showed no evidence of change.

Close examination of the shift for many biological/ecosystem indicators reveals that the timing of the shift varies among species and ecosystem parameters. The variability in the timing of the shift is related to the physiological/biological/ecological characteristics of species, to the numerical methods used to identify the shifts, and also to the different physical intermediate mechanisms by which large-scale hydro-climatic forcing influenced the regime shift.

The cause of the regime shift is related to pronounced changes in large-scale hydro-meteorological forcing. Changes (increase in sea surface temperature and change in wind intensity and direction) at the end of the 1970s in the west European basin triggered a change in the location of a biogeographical boundary along the European continental shelf, a change initiating the regime shift after 1982. In addition, large-scale hydro-climatic forcing modified local hydro-meteorological variability that affected North Sea ecosystems directly after 1987.

This shift led to marked changes in the dynamic regime of North Sea ecosystems, an exceptional period (1987–1999; see Beaugrand & Reid, 2003), which is likely to have had profound consequences for exploited resources and biogeochemical cycles.

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