

Regime shifts in marine ecosystems of the North Sea and Wadden Sea

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ABSTRACT: Wide-scale and sudden shifts in several biological and environmental systems of NW Europe have been reported in recent years, and attributed to a range of factors, both climatic and anthropogenic. To examine whether there is any evidence of coinciding region-wide environmental shifts, we gathered existing long-term data series on a wide range of physical and biological parameters from the 1960s to the present and, following the methods of a similar recent study on North Pacific regime shifts, we analysed the data using principal component analysis and regime shift analysis to identify the extent and timing of regime shifts in NW Europe. The end-point of a regime (i.e. the year) was determined using a sliding window in regime shift analysis. Additionally we applied chronological clustering to the (1) combined data, (2) biological data and (3) environmental data. In all 3 cases, the same regimes were identified. Our results indicate that substantial regime shifts occurred in the marine ecosystem in 1979 and 1988 and perhaps also in 1998, although results were less clear-cut in the latter case. These regime shifts were most evident among the biological data series, but they appeared to have been triggered by earlier shifts in a number of environmental factors. Salinity and weather conditions played an important role in the 1979 shift, while in the 1988 shift, temperature and weather conditions were the predominant factors. Our results confirm those of the North Pacific study, with concomitant changes in physical and biological indices. This indicates a shift in climate–ocean interactions throughout the entire temperate zone of the Northern Hemisphere.

KEY WORDS: North Sea · Regime shifts · Long-term data series · Principal component analysis · Regime shift analysis · Chronological clustering

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INTRODUCTION

Numerous publications have documented dramatic changes in marine ecosystems of the NW European shelf during recent decades (Appendix 1; www.int-res.com/journals/weijerman_appendix.pdf). Substantial variability has been documented in hydrographic/oceanographic relations by Svendsen & Magnusson (1992) and Ellet & Blindheim (1992), in the biomass and diversity of phyto- and zooplankton communities by Southward et al. (1995) and Edwards et al. (2002), in zoobenthic communities by Kröncke et al. (1998), in fish communities by Reid et al. (2001a), in bird communities by Swennen (1991) and in seal populations by Reijnders & Brasseur (2003). Several of these researchers have reported sudden (from one year to

the next) changes around the late 1970s and late 1980s. Reid et al. (2001b) also reported a possible third shift in 1998. These apparent shifts have been linked with climate–ocean variability such as the large-scale salinity anomaly in 1978 (Dickson et al. 1988), severe winters with low temperatures and high storm frequencies (Beukema 1990), and a drastic reduction of the Atlantic inflow in the late 1970s (Svendsen & Magnusson 1992), as well as with anthropogenic factors such as eutrophication and fisheries (OJaveer 1996). More recently, biotic changes have been linked with atmospheric modes, in particular the North Atlantic Oscillation (NAO) (Rogers 1984), which oscillates between positive and negative indices caused by a change in pressure difference between Iceland and the Azores. Hare & Mantua (2000) defined the sudden changes from one

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stable condition to another as regime shifts, a term we will use in this study.

A fundamental question in ecology is what factors drive or trigger changes in biological processes. In the late 1990s, a European project DYNAMO (Dynamics through Natural and Anthropogenic causes of Marine Organisms) was launched with the aim of improving the understanding of the natural dynamics of marine ecosystems by analysing long-term environmental and ecological data sets. The project focused on marine ecosystems of NW Europe. Results from this project indicated that large-scale changes at various levels of the marine ecosystems were taking place, and it was concluded that they were likely to have been triggered by a shift in the state of the atmosphere–ocean climate system (Philippart et al. 2000). In a different approach to the same broad questions, Ottersen et al. (2001) carried out an extensive literature review to assess the likely impact of the NAO on marine and terrestrial processes. They concluded that the NAO has a strong influence on ecological dynamics and that it causes diverse responses in ecological processes, ranging from the timing of reproduction to spatial distribution of biological communities. Scheffer et al. (2001) focused on the role of biotic interactions in driving oceanic community dynamics, and speculated that disruption of stable states by natural or anthropological events can cause shifts in species abundance on multiple trophic levels. Lindeboom et al. (1995) pointed out that marine ecosystems show large inter-annual and interdecadal variations and posited the hypothesis that the North Sea ecosystem switched from a benthic system to a pelagic system in 1978, and that a feedback mechanism acted to maintain it in that new stable state. The switch they described also led to changes in the biological and geochemical nutrient cycles, and appears to have been triggered by changes in the macro- and micronutrient ratios in incoming water, coinciding with the salinity anomaly. Bergman & Lindeboom (1999) wondered if the numerous atmospheric and climatic cycles which have been documented (Burroughs 1992) were reflected in the evident substantial variability of marine ecosystems. They considered the potential importance of the Hale cycle of 22 yr, the 11 yr sunspot cycle, and the 18.6 yr nodal cycle.

There is therefore a substantial body of evidence indicating that regime shifts occurred in the North Atlantic in the late 1970s and late 1980s, and at least 1 other study that indicates that a change occurred in 1998. The direct cause of these shifts is difficult to determine, but there are grounds for suspecting that they might be linked with climate–ocean variability. A similar study to the present one was recently carried out by Hare & Mantua (2000) in the North Pacific. They

reported evidence of regime shifts in 1977 and 1989 among a diverse set of 29 physical and 71 biological time series. In this study, we explore the timing of, and apparent cues for, sudden changes in ecological and environmental systems of the wider North Sea. Specifically, we have collected a wide range of ecological and environmental data sets from the North Sea and Wadden Sea ecosystems covering the years between 1960 and 2002. Our principal aim was to explore evidence for coincident shifts in environmental and ecological variables and to identify the years in which the largest shifts occurred. We have also attempted to identify explanatory patterns or factors by determining the physical/environmental variables that appear to contribute most to such shifts.

MATERIALS AND METHODS

We gathered long-term time series directly from scientists, from published reports, and from the Internet. Our criteria for selecting appropriate data sets were:

- Time series covering at least the last 30 yr, preferably 40 yr
- Large spatial spreading, i.e. including data from the whole North Sea, Skagerrak, German Bight and Wadden Sea
- No or few missing values in the data set
- No obvious anthropogenic cause for sudden changes in a data series
- Time series comprising multiple trophic levels and different environmental variables

With these criteria we aimed to select a diverse set of around 100 variables. Fig. 1 shows the spatial distribution of the variables in the North Sea and Dutch Wadden Sea. Variables are numbered as in Table 1. The availability of data sets meeting all criteria limited our study to 78 data sets: 28 environmental data sets comprising atmospheric and oceanic variables, and 50 biological time series representing a very wide range of marine organisms from phytoplankton to top-level predators. Appendix 2 (www.int-res.com/journals/weijerman_appendix.pdf) presents the time series used and their sources, and explains why certain data sets were excluded from some analyses.

From the literature it became clear that climate conditions in winter months have the greatest influence on biological processes (e.g. Beare & McKenzie 1999, Beukema et al. 2002) and we therefore included mostly winter averages for the physical parameters. For biological variables we used either spring/summer means or annual averages. None of the data sets have been smoothed, other than taking the seasonal or annual average. To reduce the effect of outliers and to

linearize the relationships between the biological variables, a logarithmic transformation was applied to all biological variables and 2 environmental time series (summer storms and the number of days with frost).

Following the approach of Hare & Mantua (2000) we analysed the data using 2 statistical methods: principal component analysis (PCA) and regime shift analyses (RSA) as employed by Ebbesmeyer et al. (1991).

The PCA was used to determine a general pattern in the time series. As our original data series are measured in different units and have a wide range in variation, the PCA was based on the correlation coefficient instead of the covariance coefficient (Jolliffe 2002). We concentrated on 3 outputs of PCA: (1) the principal components (PCs, also called the PC scores or eigenvectors) which, plotted against time, show the underlying pattern of a specific PC and thus if and when a sudden change occurred; (2) loadings, which show the extent to which original variables are related to PCs; and (3) the eigenvalues, which show how much of the variance in the total data is explained by each PC. We wanted to account for at least 40 % of total variation in the original variables and based on that we determined the number of PCs to use in each case.

Because some of the biological time series only started in the 1970s, we first wanted to know to what

extent the PCA output would be influenced by those shorter time series. Missing values in PCA are replaced by column (= variable) averages, resulting in less variation in the data. We did this by comparing (1) the PCA results from the full biological data set (48 variables, 42 years), with (2) the PCA results from all biological data sets but starting in 1970, with (3) the PCA results of only those data sets with not more than 10 missing values (resulting in 34 data sets), and with (4) the PCA results of the same 34 time series but now only taking into account the years 1970 to 2002. The resulting patterns of the PCs of all 4 PCA were very similar; only the amount of variance explained by the first 2 PCs differed by up to 6%. As we were most interested in the underlying pattern of the whole ecosystem and expected the first shift in the late 1970s, we decided to continue further analyses with the complete data set but starting in 1970, as these seemed to be the most robust data. In order to compare these PCA results with the environmental time series, we used only the data from 1970 onwards for all variables.

The second statistical model is the so-called step analysis or regime shift analysis (Ebbesmeyer et al. 1991). Based on the results of the PCA we used this method to identify the year(s) in which largest shifts occurred by calculating step-magnitude for 5 con-

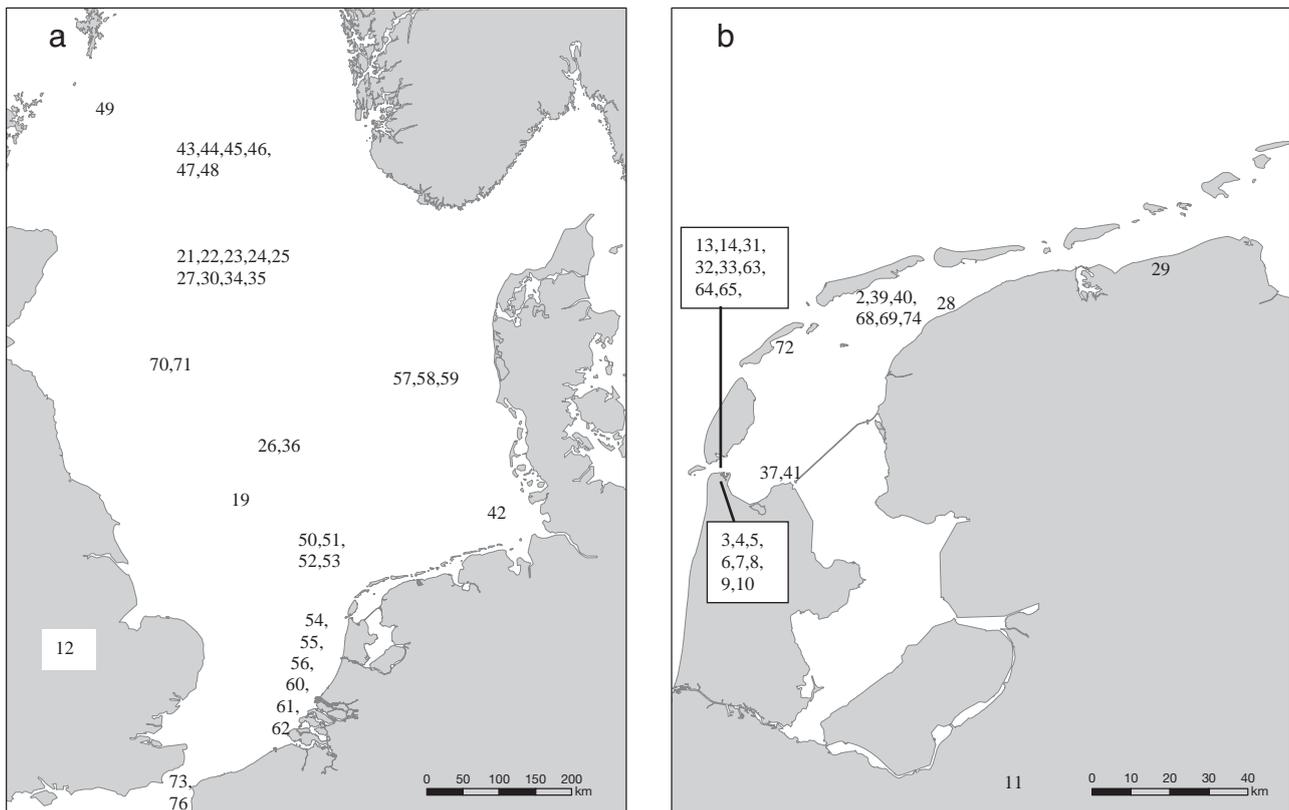


Fig. 1. Spatial distribution of sample locations in (a) North Sea and (b) Dutch Wadden Sea. Variables numbered as in Table 1

Table 1. Differences of mean values of individual time series between 2 regimes (see Step 3 in regime shift analysis in 'Materials and methods'). 1979 change is difference between 1969 to 1978 (Regime I) and 1980 to 1989 (Regime II); 1988 change is difference between 1978 to 1987 (Regime II) and 1989 to 1998 (Regime III). Differences only calculated when >5 yr before and >5 yr after year of change for any given time series. Detailed description, pattern of each time series and its source are given in Appendix 2. NCP: Netherlands Continental Plateau

Var. no.	Abbreviation	Description	1979 change Mean of Regimes I–II	1988 change Mean of Regimes II–III
1	NAOWIN	North Atlantic Oscillation winter index (Dec, Jan, Feb, Mar average)	0.68	0.77
2	WADMHT	Annual mean high tide in Wadden Sea	1.44	0.07
3	WINDIR	Prevailing wind direction in degrees (360° = N, 270° = W, 180° = S, 90° = E) in De Kooy (North Holland)		
4	WINSPE	Mean annual wind speed in De Kooy	0.77	0.20
5	AIRTEMP	Mean annual air temperature in De Kooy	–1.26	–0.47
6	SUNSHI	Mean annual air temperature in De Kooy	–0.34	1.56
7	PRECIP	Total annual sunshine duration in De Kooy	–0.49	1.81
8	SAP	Total annual precipitation amount in De Kooy	1.05	–0.25
9	CLOUD	Mean annual surface air pressure in De Kooy	0.25	1.12
10	Log_SUMSTORM	Mean annual cloud cover in De Kooy	0.16	–0.46
11	Log_V_Ynsen	No. of days in summer (Jun, Jul, Aug) with wind speed >10.8 m s ⁻¹ or >6 Beaufort	–0.77	–0.24
12	ASTCE	Total days with frost (i.e. min. temperature <0°C) from Nov to Mar in De Bilt (Netherlands)	0.05	–0.99
13	WZTEMPWIN	Average surface air temperature in central England	0.09	2.88
14	WZSAL	Mean winter sea-surface temperature at Marsdiep, Wadden Sea (Dec, Jan, Feb, Mar)	0.02	1.02
15	SSN	Mean annual sea-surface salinity at Marsdiep, Wadden Sea	–1.47	0.93
16	EA	Sunspot no.	0.61	–0.17
17	EA_JET	East Atlantic teleconnection pattern index (Sep to Apr)	1.65	–0.01
18	SCAN	East Atlantic Jet pattern index (Apr to Aug)	0.87	1.19
19	WAVE_WIN	Scandinavian teleconnection pattern, indices all months except Jun and Jul	–0.09	–0.63
20	SOLCON	Wave height (m) at Buoy K13 in North Sea (winter average)		–0.16
21	SST_NS	Solar constant derived from solar irradiance with interpolated monthly values	2.94	1.23
22	SST_WIN	Annual average sea-surface temperature in North Sea (51 to 62° N, 4° W to 12° E)	–0.21	2.11
23	SST_SUM	Mean winter sea-surface temperature in North Sea (50 to 60° N, 0 to 4° E) (Jan, Feb, Mar)	–0.64	1.89
24	SLP	Mean summer sea-surface temperature in North Sea (50 to 60° N, 0 to 4° E) (Jun, Jul, Aug)	–0.07	1.48
25	N/P_JFM	Mean sea-level pressure in North Sea (0 to 6° E, 50 to 60° N)		–0.17
26	SAL_NS	Nitrate–phosphate relation in southern North Sea (Jan, Feb, Mar) (ICES Quadrant IVb 50 to 55° N, 0 to 5° E)	1.24	1.31
27	WINSP_NS	Annual average sea-surface salinity in southern North Sea (ICES Quadrant IVb 50 to 55° N, 0 to 5° E)	–1.43	–0.91
28	FRMARSH	Annual mean wind speed (m s ⁻¹) over North Sea	1.33	1.03
29	GRMARSH	Outer border marshland area along coast of Friesland (m from dyke)	5.10	1.44
30	PHYTWIN	Outer border marshland area along coast of Groningen (m from dyke)	–7.70	0.48
31	CHLOR_A	Annual winter (Dec, Jan, Feb, Mar) phytoplankton colour averaged for North Sea	–0.22	0.71
32	SPM	Annual average chlorophyll <i>a</i> concentration in Marsdiep tidal inlet	1.76	–0.18
33	PHAEOBLO	Suspended particulate matter estimated from Secchi disk at high tide in Marsdiep (Jul, Aug, Sep)	–1.07	0.27
34	CALSUM	Length of <i>Phaeocystis</i> spp. bloom periods (cells > 1000 cm ⁻³) in Marsdiep		2.03
35	COPEP	Abundance of total <i>Calanus</i> spp. for North Sea, summer averages (Jun, Jul, Aug, Sep)	0.15	–1.71
36	CERMAC	Abundance of total copepods for North Sea, summer averages (Jun, Jul, Aug, Sep)	0.12	–0.30
37	POLYCHAET	Frequency of occurrence of dinoflagellate <i>Ceratium macroceros</i> in southern North Sea in continuous plankton recorder samples	–5.48	2.19
38	BIVALVE	Late winter polychaete biomass in Balgzand, Wadden Sea	2.80	1.66
		Late winter bivalve biomass (mg AFDW m ⁻²) in Balgzand, Wadden Sea	1.74	0.24

Table 1 (continued)

Var. no.	Abbreviation	Description	1979 change Mean of Regimes I–II	1988 change Mean of Regimes II–III
39	BIO_CEREDU	Biomass of cockle <i>Cerastoderma edule</i> flesh (billion kg) in Wadden Sea	0.10	-0.39
40	CAT_CEREDU	Catch of cockle <i>Cerastoderma edule</i> flesh (billion kg) in Wadden Sea	1.57	0.10
41	GASTRO	Late winter gastropod biomass in Balgzand, Wadden Sea	1.36	0.03
42	CRACRA	Mean >54 mm year class abundance of brown shrimp <i>Crangon crangon</i> on the west coast of Schleswig-Holstein, Germany	0.33	-1.92
43	LANDCOD	International landing of cod from ICES Quadrants III, IV, VIId	-0.27	-5.50
44	sqrtLANDHER	International landing of herring from ICES Quadrants III, IV, VIId	0.60	1.23
45	LANDHAD	International landing of haddock from ICES Quadrants III, IV, VIId	-1.94	-2.42
46	LANDWHIT	International landing of whiting from ICES Quadrants III, IV, VIId	-2.53	-1.87
47	LANDSOLE	International landing of sole from ICES Quadrants III, IV, VIId	0.02	1.14
48	LANDPLAI	International landing of plaice from ICES Quadrants III, IV, VIId	4.02	-1.75
49	HORSE	Catches of horse mackerel (1000 t) from NE Atlantic	-1.28	6.53
50	NOR_POU	International bottom trawl survey in North Sea: Norway pout recruitment yield (avg. no. h ⁻¹ fishing)		0.03
51	SPRAT	International Bottom Trawl Survey in North Sea: sprat recruitment yield (avg. no. h ⁻¹ fishing)		0.90
52	COD	International Bottom Trawl Survey in North Sea: cod recruitment yield (avg. no. h ⁻¹ fishing)		0.07
53	WHIT	International Bottom Trawl Survey in North Sea: whiting recruitment yield (mean no. h ⁻¹ fishing)		1.29
54	OSMEPE	Relative abundance of smelt <i>Osmerus eperlanus</i> in NCP		-0.34
55	LIMLIM	Relative abundance of dab <i>Limanda limanda</i> in NCP		1.12
56	LIPLIP	Relative abundance of sea-snail <i>Liparis liparis</i> in NCP		-2.20
57	CLUHAR	Relative abundance of herring <i>Clupea harengus</i> in North Sea (including Skagerrak/Kattegat)		1.86
58	GADMOH	Relative abundance of cod <i>Gadus morhua</i> in North Sea (including Skagerrak/Kattegat)		0.31
59	SOLVUL	Relative abundance of sole <i>Solea vulgaris</i> in North Sea (including Skagerrak/Kattegat)		-1.41
60	BUGLUT	Relative abundance of solenet <i>Buglossidium luteum</i> in NCP		3.22
61	ARNLAT	Nos. ha ⁻¹ of scald fish <i>Arnoglossus laterna</i> in NCP	0.13	2.72
62	ECHVIP	Nos. ha ⁻¹ of lesser weever <i>Echiichthys vipera</i> in NCP	0.60	2.52
63	PLEPLA	Recruit numbers d ⁻¹ of plaice <i>Pleuronectes platessa</i> in Marsdiep, Wadden Sea	2.51	-1.01
64	CLUPHA	Recruit numbers d ⁻¹ of herring <i>Clupea harengus</i> in Marsdiep, Wadden Sea	4.89	0.98
65	ALOFAL	Recruit numbers d ⁻¹ of twait chad <i>Alosa fallax</i> in Marsdiep, Wadden Sea	0.49	0.80
66	POLPOL	Recruit numbers d ⁻¹ of pollack <i>Pollachius pollachius</i> in Marsdiep, Wadden Sea	0.15	-0.72
67	MERMER	Recruit numbers d ⁻¹ of whiting <i>Merlangius merlangus</i> in Marsdiep, Wadden Sea	1.22	-0.50
68	OYSTERC	Total calculated bird days in January for oystercatcher (in Dutch Wadden Sea)	0.46	0.35
69	WORM.EAT	Total calculated bird days in January for worm-eating wader species in Dutch Wadden Sea	-4.12	1.14
70	BRABRA	Number of dark-bellied Brent geese <i>Branta branta bernicla</i> in western Europe based on sightings and from 2000 to 2002 on estimation	4.04	2.87
71	BRA_CHICK	Percentage of first year dark-bellied Brent geese chicks in western Europe	-0.38	0.23
72	FLEDGE	Number of eider duck fledglings on Dutch island of Vlieland	2.47	
73	SEAL	Stranding of total seal species on beaches of southern North Sea	1.95	0.01
74	SEALPUPS	Percentage counted pups in total number of sightings of harbour seal <i>Phoca vitulina</i> in Wadden Sea	0.35	3.48
75	PHOVIT	Population count of the harbour seal <i>Phoca vitulina</i> in the Dutch Wadden Sea	0.60	1.52
76	PHOPHO	Sightings of porpoises <i>Phocoena phocoena</i> along Dutch and Belgium North Sea coastlines (corrected h ⁻¹)	14.10	4.85

secutive years around each putative shift (1978 or 1979, 1988 or 1989, 1997 or 1998) resulting in a step-magnitude of the expected year of the shift (based on the literature) and the 2 years before and after each year. This gave us an objective method of identifying the years with the highest step-magnitude. The regime shift analysis technique is described in detail in Ebbesmeyer et al. (1991) and Hare & Mantua (2000); the basic procedure is:

Step 1. For each time series, calculate the mean (of the entire time series) and the standard deviation of Regimes 1 and 2.

Step 2. Normalise each time series by subtracting the mean value and dividing by the appropriate standard deviation. The underlying idea of using 2 different standard deviations is that a sudden change in the system might result in an increase in variation. However, in this analysis we are only interested in the absolute value of the shift, and not in an increase of variance.

Step 3. Because we are not interested in the sign of the step, some series are reversed such that the step has the same sign in all time series. A series was reversed ($Y_t = -1 \times Y_t$ for all years t) if the mean value in the first regime was higher than in the second regime. Therefore, we will always find an increasing step.

Step 4. Calculate the average value for each year using all the (modified) time series.

Step 5. Calculate the standard error for each year using $s/n^{0.5}$, where n is the number of time series in a year and s the standard deviation in that year.

Step 6. Calculate regime averages using the mean values (obtained in Step 3). The overall step-magnitude can be defined as the difference between these 2 mean values.

To visualise the change, a smoother can be fitted or the regime averages can be plotted as horizontal lines. To assess whether the change in the regime averages is an artifact of the algorithm or not, (1) the width of the standard errors can be inspected, and (2) one can examine the change in the regime averages for different values of the time of shift (e.g. compare results using a sliding window).

The statistical software package Brodgar (available at: www.brodgar.com) contains an implementation of this algorithm, and was used here. To apply RSA the data were grouped into regimes prior to and after the suspected shift, with each regime being of equal number of years—10 yr in the case of the suspected 1979 and 1988 shifts, and 4 to 6 yr in the case of the 1998 shift. Following the approach of Ebbesmeyer et al. (1991), we only included time series for which there were at least 5 data points per regime. Besides the difference between the mean values of the 2 regimes (see Step 6 of the RSA algorithm above), it is also interest-

ing to examine the differences in the mean values of the individual time series between the 2 regimes. These are obtained in Step 3 and shown in Table 1.

The use of RSA and its combination with PCA has recently been criticized by Rudnick & Davis (2003). Using randomly generated time series (red noise) they found regime shifts with the methodology described above. In a follow-up paper, Hare & Mantua (in press) defended their approach. Because of this, we decided to apply another statistical technique, capable of detecting breakpoints in multivariate time series, namely chronological clustering. This technique is described in Legendre et al. (1985), Bell & Legendre (1987) and Legendre & Legendre (1998). The first 2 studies can be downloaded from www.fas.umontreal.ca/biol/legendre/reprints/.

The disadvantage of clustering techniques applied to time series data is that they end up in groups of non-sequential years, which makes the interpretation difficult. Chronological clustering results in groups of sequential years, and therefore allows the identification of breakpoints. At this point, it is interesting to mention that chronological clustering applied to the North Pacific time series data analysed in Hare & Mantua (2000) identifies the same regime shifts, namely in 1977 and 1989 (see the Brodgar manual: www.brodgar.com).

Before this technique can be applied, the measure of association between years, the significance level alpha and the connectedness has to be determined. Alpha can be considered as a clustering-intensity parameter. Small values of alpha (0.01 to 0.1) show the most important breakpoints in the time series, whereas larger values (0.1 to 0.3) show small-scale variation. Legendre et al. (1985) argued that using the same connectedness level (e.g. 50%) and different values for alpha is the most informative, and this approach was followed here. Legendre et al. (1985), and Legendre & Legendre (1998) used zoobenthic data, for which the Whittaker index of association is a sensible choice to define similarity between years. For our data, this is not appropriate because some of the variables take negative values. Therefore, we first standardised each variable, and then used the Euclidean distance function to calculate the (dis)similarity between years. The software package Brodgar was used for these calculations.

RESULTS

Principal component analysis

The eigenvalues from PC1 to PC10 of PCA using the environmental and biological time series com-

binned show that the first 3 PCs explained 43% of the variance. PC1, with an eigenvalue of 21.1%, can be interpreted as a pattern with an abrupt change in 1987–1988, where values switch from positive to negative or as a pattern with 3 regimes: positive until 1979, then a gradual decline until 1988, after which it was strongly negative (Fig. 2). Almost half of the variables (47%) were strongly related to PC1, as they had loadings $>|0.5|$, and as much as 71% had loadings of $>|0.3|$. These variables were evenly distributed over the food chain, with highest loadings found for a number of variables relating to fish species (positive loadings for the landing of cod, haddock and whiting and negative for the abundance of lesser weever, solenet, scaldfish). High negative loadings were also found for the abundance of polychaetes, for the number of strandings of seals in the southern North Sea, and for the number of Brent geese chicks in western Europe. The environmental variable with the strongest positive relation with the first PC was salinity in the North Sea, and the variables most strongly negatively related were temperature indices (surface temperature in De Kooy, average surface temperature over central England, and sea-surface temperature of the North Sea).

PC2, eigenvalue 12%, showed 2 abrupt changes dividing the PC into 3 clear regimes: negative until 1979, then a switch to strongly positive until 1989, after which it flipped back and forth (Fig. 2). This PC had

high values before 1988, after which the scores became rather small. Of the variables, 52% had a relationship with PC2; of these, 23% had a loading $>|0.5|$. Ecological variables with the highest positive loading were chlorophyll *a* concentration in the Wadden Sea, and the number of plaice and herring recruits in the Marsdiep (an inlet in the western Wadden Sea). Variables with the highest negative loading were the frequency of occurrence of the dinoflagellate species *Ceratium macroceros*, the catches of horse mackerel in the NE Atlantic, and the abundance of worm-eating wader birds. The physical variable with the strongest positive association with PC2 was the solar constant, and the strongest inverse relationships were with North Sea winter sea-surface temperature and Wadden Sea salinity.

PC3, with an eigenvalue of 10%, was the first to show an abrupt change in 1998, but showed no shift in 1978 or 1979 and in the late 1980s became only briefly negative (Fig. 2). Of the 73 variables, 33 had a strong association with Axis 3, i.e. loadings $>|0.3|$, 17 with a loading higher than $|0.5|$. The biomass of cockles in the Wadden Sea and the summer abundance of copepods *Calanus* spp. were inversely related to PC3; the abundance of herring in the North Sea and the winter phytoplankton abundance were positively related. Among environmental variables, mean high tide in the Wadden Sea and wind direction in De Kooy (a station in North Holland, close to the

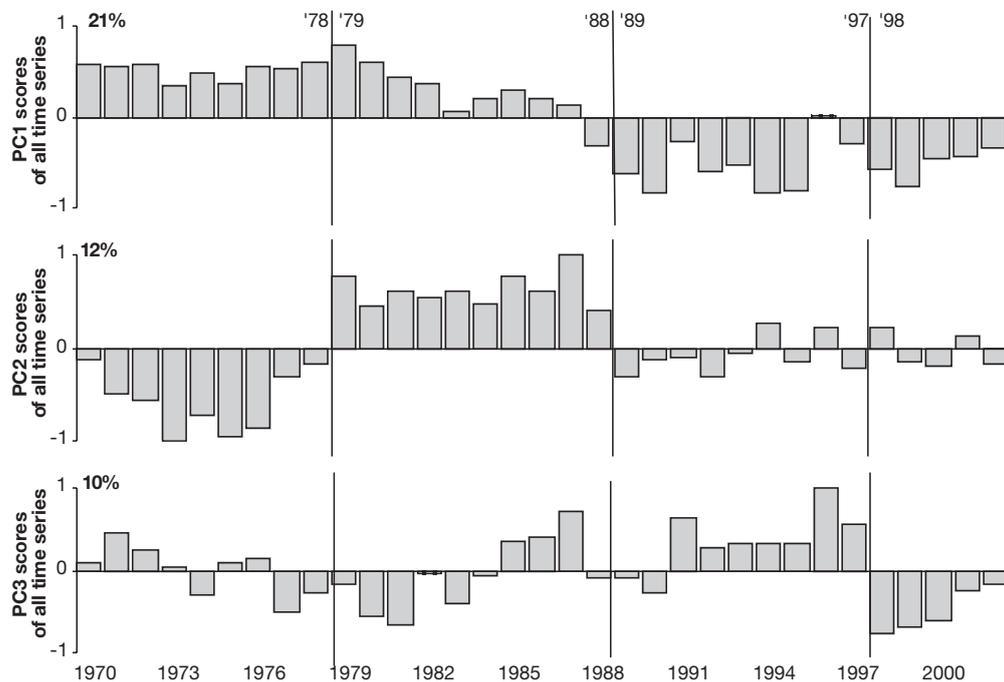


Fig. 2. Principal component (PC) scores of principal component analysis (PCA) of environmental and biological time series combined from 1970 to 2002. Eigenvalue given as percentage in top left-hand corner for each score series

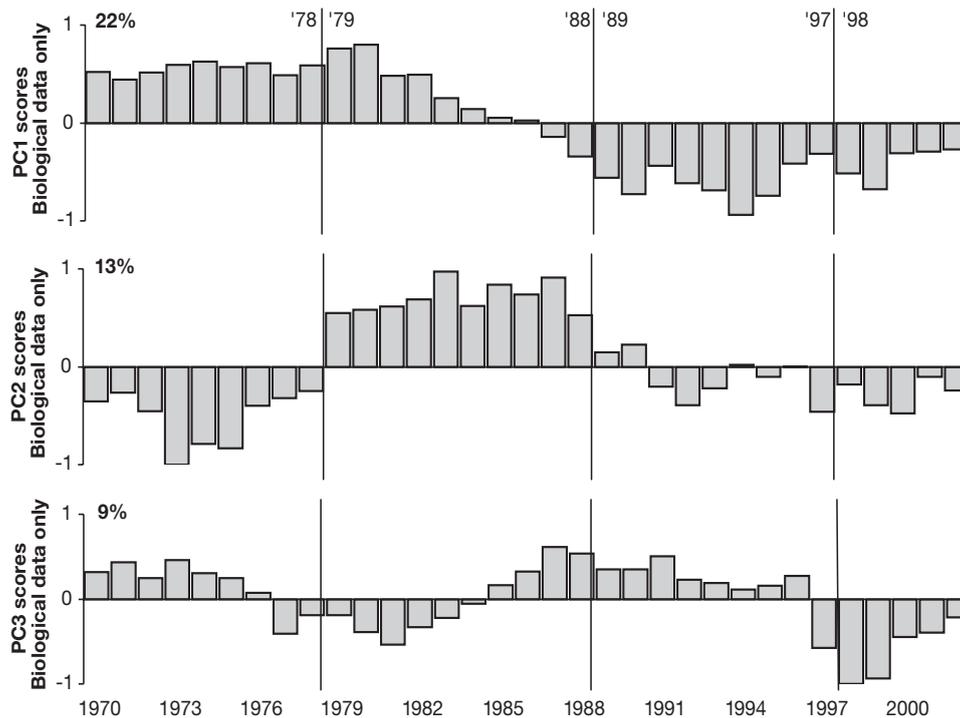


Fig. 3. Principal component (PC) scores of PCA of 46 biological time series from 1970 to 2002. Eigenvalue given as percentage in top left-hand corner for each score series

coast) had the strongest negative relationship with PC3, and surface air pressure the strongest positive relationship.

In summary, PC1 appeared to show the proposed 1987 or 1988 shift in the North Sea and Wadden Sea most strongly. PC2 indicated abrupt changes in 1979 and 1989, and a possible third shift in 1998 might be indicated by PC3.

Biological time series

The PC scores of the PCA of biological variables only (Fig. 3) showed a large similarity with those of the PCA of the combined data sets (Fig. 2). Eigenvalues were similar too so again we used the first 3 PCs, which explained 44% of the variance. Note that the biological-only PCs were noticeably smoother (more gradual year-to-year change) than combined PCs. Only PC2 showed an abrupt change in 1979.

Regime shifts in 1979 and 1988 were clearly present in PC2, but the possible regime shift in 1998 was not obvious in any of the 3 PCs. Variables with high loadings were similar to those of the combined environmental and biological data sets. The ordination diagram in Fig. 4 showed 3 distinct regimes: 1970 to 1978 in one cluster, 1979 to 1988 in another, and 1989 to 2002 in a third cluster.

Environmental time series

PC1 and PC2 explained 48.7% of the variation. Fig. 5 shows a shift in 1987 from a predominant positive phase to a negative phase in the first PC (eigenvalue 28%). The second PC (eigenvalue 17%) alternated between positive and negative, with changes coinciding with the proposed 1979, 1988 and 1998 shifts (Fig. 5). As the pattern of this axis was predominantly related to local climate indices (surface air pressure, cloud cover and amount of precipitation in De Kooy: loadings $> |0.80|$), we also included a third axis. The third PC scores showed an abrupt change in 1979, changing from positive to negative (although in 1980 and 1981 briefly flipping back to positive), and then in 1989 returning to the pre-1979 state for a few years. In conclusion, climate indices alone appeared to show abrupt changes in 1979 and 1988, but these seemed to be less strong than those of the biological variables.

Out of 25 physical variables, 15 had a loading $> |0.50|$, indicating a strong relationship with the pattern of the first PC. The parameters that had the strongest relationship (loadings $> |0.80|$) were surface air temperature in De Kooy, winter temperature in the Wadden Sea, sea-surface temperature in the North Sea, the NAO winter index, and mean high tide in the Wadden Sea (all negative loadings). The number of days with frost was the only variable with a large posi-

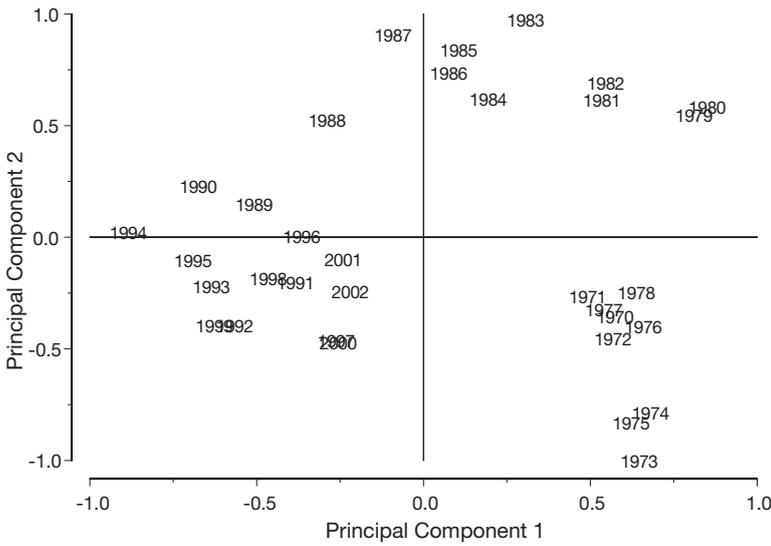


Fig. 4. Clusters of samples in PCA ordination diagram of 46 biological standardised time series from 1970 to 2002

tive loading. As only weather variables (surface air pressure, cloud cover and precipitation) from 1 station were highly related to the second axis, it was very likely related to conditions on a more local scale. Salinity in the North Sea and sunspot number were positively related to PC3, as was the winter sea-surface temperature of the North Sea. Variables with high negative loadings were average surface temperature

in central England and the winter N:P ratio in the North Sea.

The ordination diagram of environmental variables alone (Fig. 6) did not show the 3 clusters evident in the biological-only biplot (Fig. 4).

Regime shift analyses

As PCA results appeared to corroborate the possible shifts of 1978 or 1979, 1988 or 1989, and (less clearly) 1998 or 1999, we based the regime shift analysis around those years. Using a sliding window approach, we determined the exact end-point of the regime shift (bold in Table 2) represented by the largest calculated step-magnitude between 2 regimes (Step 6 of the RSA algorithm in 'Material and methods'). Results are shown in Table 2.

In agreement with our assessment of the PCA results, the first step was largest in 1979, the second in 1988, and the third in 1998. Table 1 shows the step-magnitudes for each individual time series in both 1979 and 1988 (i.e. the change between the regime before and after years 1979 and 1988). As we only had a limited number of data points for the 1998 shift, we shall not go into more detail for that shift. In both 1979 and 1988 there was an upwards step (in both cases more negative values in the pre-shift compared

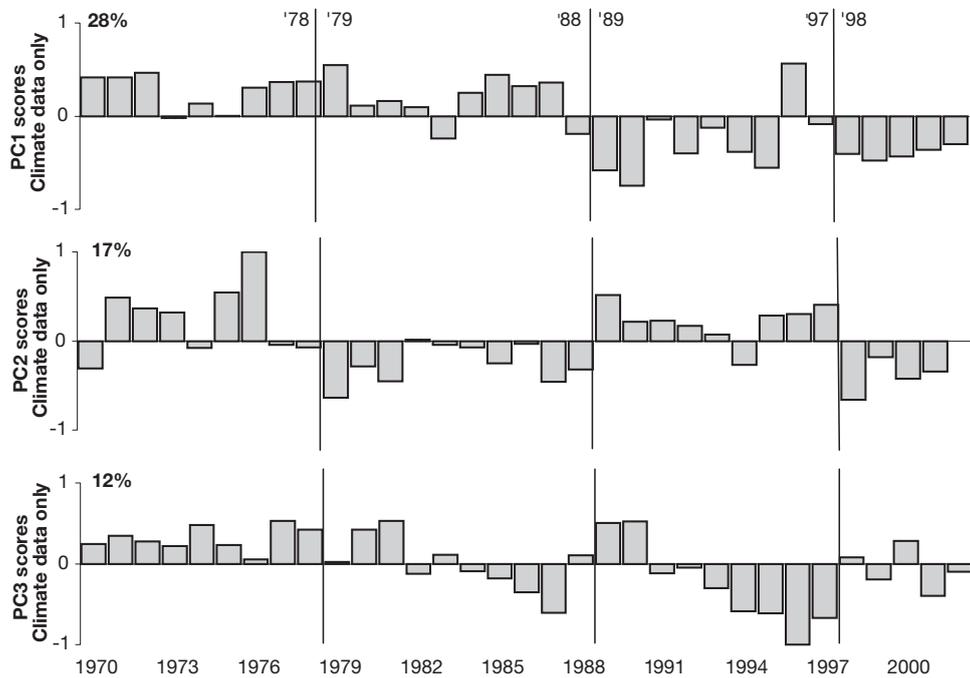


Fig. 5. Principal component (PC) scores of PCA of 25 climate time series from 1970 to 2002. Eigenvalue given as percentages in top left-hand corner for each score series

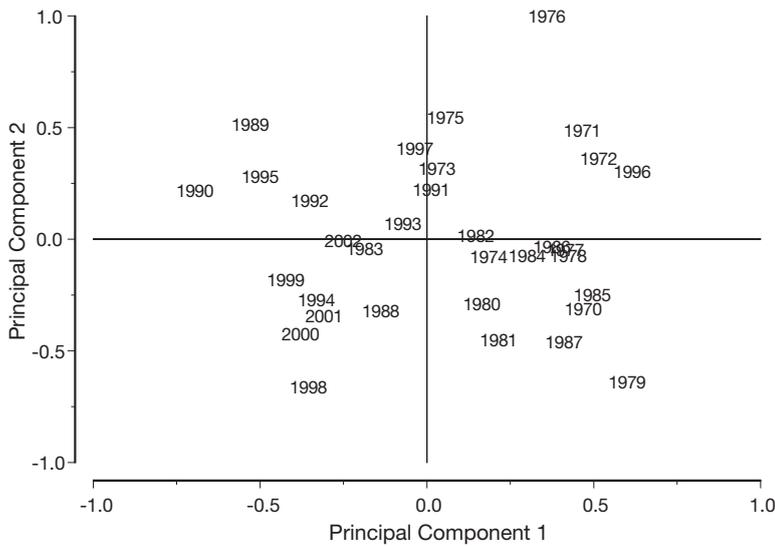


Fig. 6. PCA ordination diagram of 25 environmental standardised time series from 1970 to 2002

to the post-shift regime, Table 1). This indicates a general upwards trend which corresponds with the main underlying pattern of PC1 (Fig. 2).

Step-magnitudes of 1979 and 1988 are presented in Fig. 7. Additionally we added a smoothing curve (obtained by additive modelling; Hastie & Tibshirani 1990) to aid visual interpretation. Note that the SE bars before and after the shift in Fig. 7 do not overlap.

Table 3 shows the results of the stepmagnitudes for the biological and climate time series separately. The largest shift size in the climate data was 1 yr before the largest shift size in the biological time series. This was true for both the first and the second step. In addition, both steps were more prominent (of larger magnitude) in biological variables only compared with environmental variables only (see also Fig. 8, results shown for 1988 shift).

Fig. 9 shows the contribution of the variables, i.e. individual time series (description of abbreviations and

variable nos. as in Table 1), to step-magnitude in 1979 and 1988. As can be seen, the contribution of individual variables to the shift size is fairly diverse.

The 5 climate and 10 biological variables displaying the largest difference between 2 regimes (largest step magnitude) are summarized in Table 4.

In the 1979 regime shift, the solar constant, the East Atlantic teleconnection pattern and the mean high tide in the Wadden Sea all suddenly increased, whereas salinity in both the North Sea and the Wadden Sea suddenly decreased. The number of porpoise sightings in the North Sea greatly increased between before and after 1979, followed by area of marshland, the abundance of a dinoflagellates species (*Ceratium macroceros*), some fish species, worm-eating wader birds, and the dark-

Table 3. Regime shift analysis using sliding window approach to calculate the step magnitudes of biological-only and environmental-only time series by averaging the annual means of 10 yr before and 10 yr after the year of suspected regime shift. No. of standardised time series used for calculation are given in parentheses. **Bold** indicates end-point of regime shifts

	Biological variables only Magnitude	Environmental variables only Magnitude
Step I		
1976	1.49 (22)	1976 0.85 (24)
1977	1.59 (28)	1977 0.90 (25)
1978	1.70 (29)	1978 0.93 (25)
1979	1.90 (37)	1979 0.79 (25)
1980	1.67 (38)	1980 0.71 (25)
1981	1.62 (38)	1981 0.68 (25)
Step II		
1986	1.37 (48)	1986 0.79 (27)
1987	1.37 (48)	1987 0.92 (27)
1988	1.44 (48)	1988 0.91(27)
1989	1.43 (47)	1989 0.82 (27)
1990	1.29 (45)	1990 0.68 (27)

Table 2. Sliding window approach for calculating step magnitudes by averaging annual means of 10 yr before and 10 yr after year of suspected regime shift. For late 1990s only a limited number of years were available to calculate average step magnitude (no. of years given in parentheses). No. of standardised time series used for calculation includes environmental and biological time series out of total of 75 (25 environmental and 50 biological). **Bold** indicates end-points of regime shifts

Step I	Magnitude	No. of time series	Step II	Magnitude	No. of time series	Step III	Magnitude	No. of time series
1976	1.08	46	1986	1.16	75	1996	1.10	52 (6 yr)
1977	1.20	53	1987	1.21	75	1997	1.39	45 (5 yr)
1978	1.33	54	1988	1.25	75	1998	1.61	45 (4 yr)
1979	1.42	62	1989	1.21	74			
1980	1.26	63	1990	1.03	71			
1981	1.16	62	1991	1.00	70			

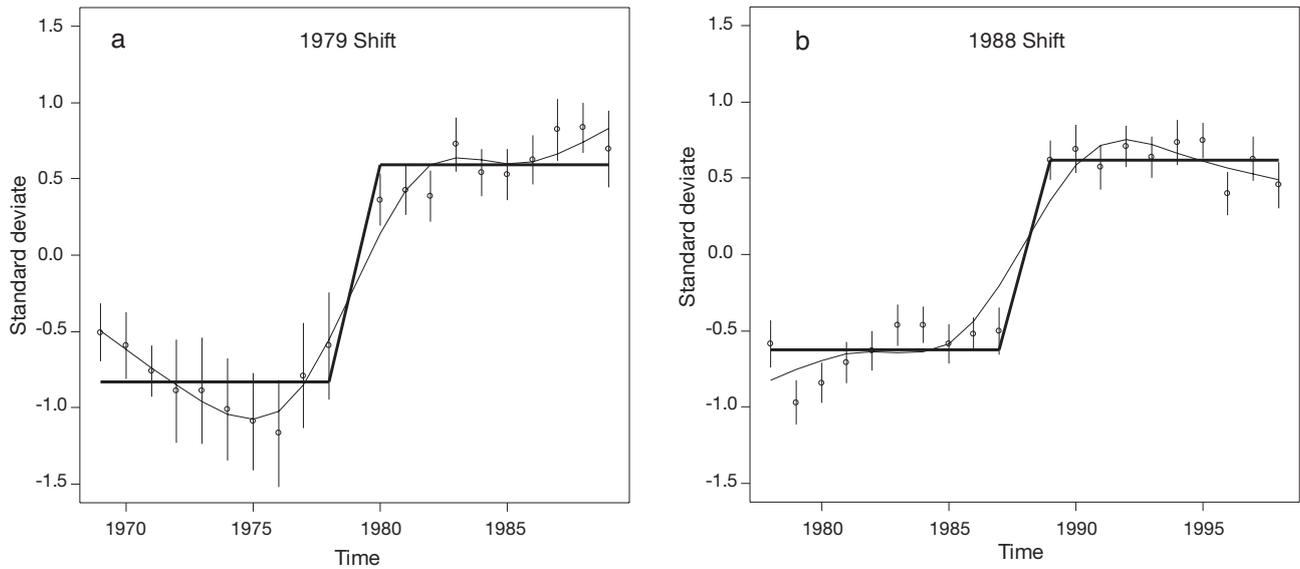


Fig. 7. Results of step analyses showing 2 consecutive upward steps in (a) 1979 and (b) 1988. Circles represent annual means of standardised time series, and the bars represent ± 2 SE. Continuous line is a generalized additive model (GAM) with 6 df

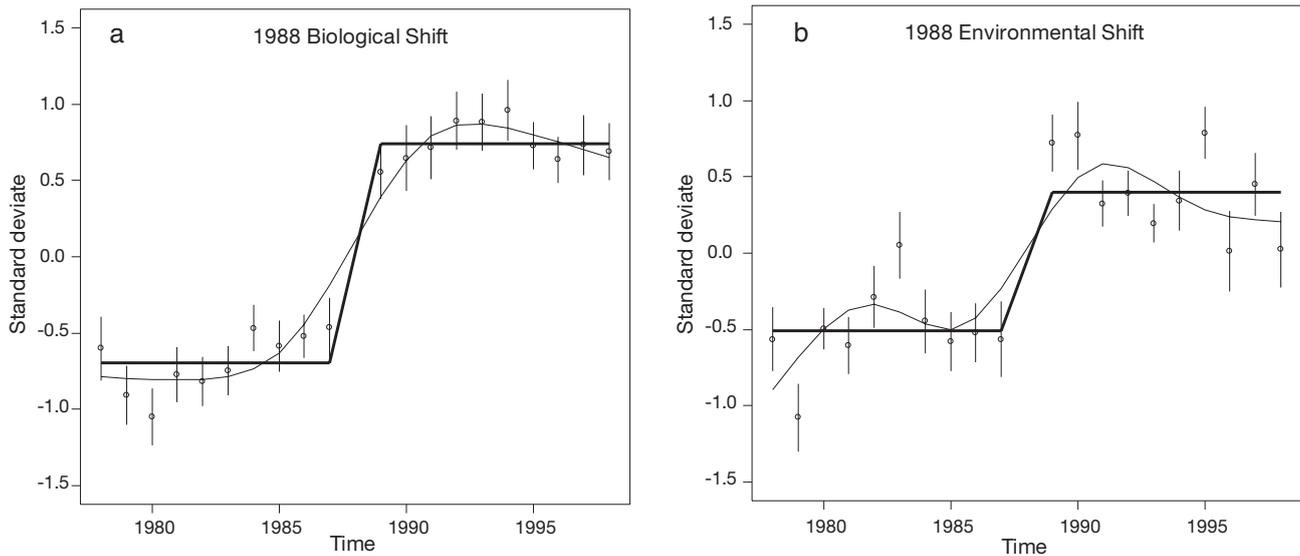


Fig. 8. Results of 1988 regime shift analyses for (a) biological and (b) environmental variables. Circles represent annual means of standardised time series, and the bars represent ± 2 SE. Continuous line is a generalized additive model (GAM) with 6 df

bellied Brent geese, and to a lesser extent the biomass of polychaetes and the landing of whiting. The 1988 regime shift seems to be triggered by climate variables as only temperature indices showed a sudden jump. Among the biological variables, increased abundance of several fish taxa coincided with the 1988 regime shift.

Chronological clustering

Combined data

The results for the combined biological and environmental data are presented in Fig. 10. They can be interpreted as follows: 5 lines correspond to different

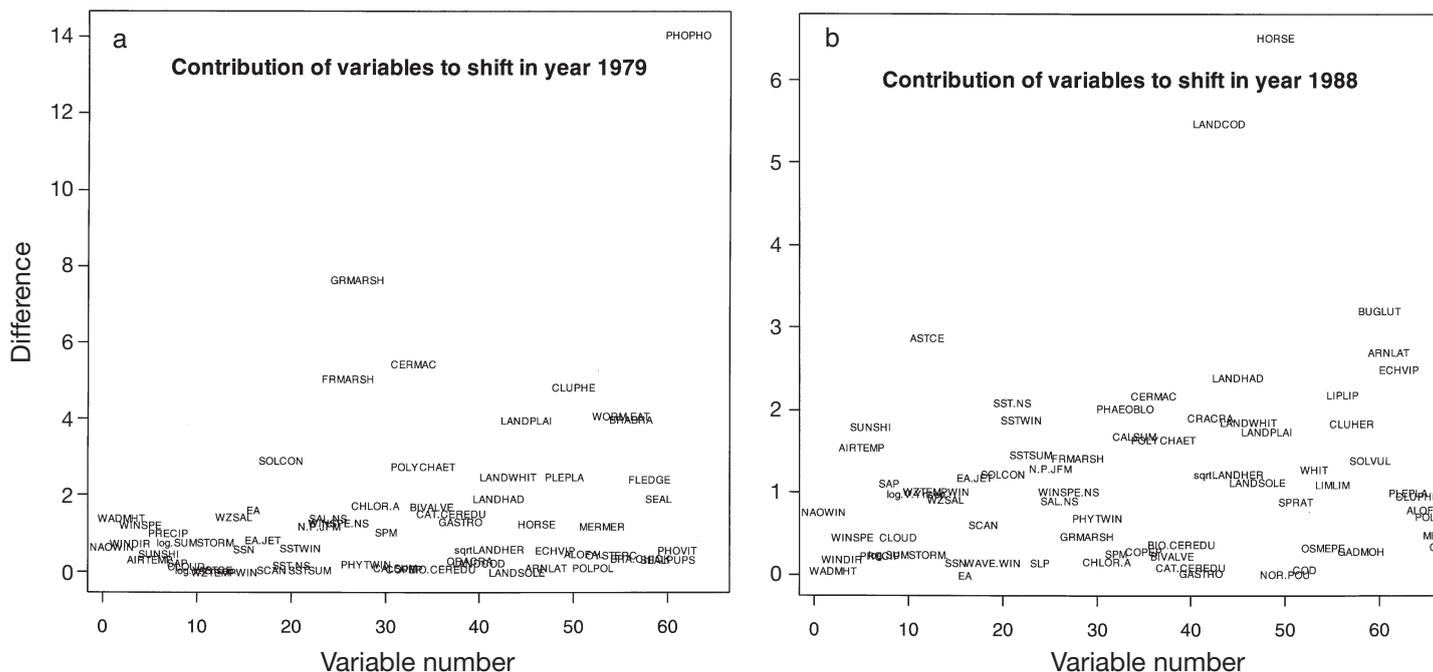


Fig. 9. Contribution of individual standardised time series to average absolute step magnitude in (a) 1979 and (b) 1988. See Table 1 for description of abbreviations and variable no.

values of alpha, the clustering intensity parameter. The line with alpha = 0.01 provides a general overview and shows the most important breakpoints. The numbers on each line correspond to groups of years, and a vertical line represents the start of a new group. Hence, for the combined data, there were major breakpoints in 1979 (or 1978) and 1988 (or 1987). For larger values of alpha, the same breakpoints were obtained, but there was clearly more variation in the 1980s. An *a priori* test (Legendre et al. 1985) showed that years in

Group 1 were not only different from Group 2, but also from Group 3. Hence, chronological clustering revealed 3 different regimes in the combined biological and environmental variables.

Biological data

The results of chronological clustering applied to the biological data are presented in Fig. 11. The years 1979

Table 4. Time series with the largest differences between 2 consecutive regimes. Difference in 1979 is between 1969 to 1978 (Regime I) and 1980 to 1989 (Regime II), 1988 difference is between 1978 to 1987 (Regime II) and 1989 to 1998 (Regime III)

Variables with largest difference in 1979	Shift I–II	Variables with largest difference in 1988	Shift II–III
Solar constant	2.94	Average surface air temperature over central England	2.88
Teleconnection pattern in East Atlantic	1.65	Sea-surface temperature in North Sea	2.11
Salinity in Wadden Sea	-1.47	Winter sea-surface temperature in North Sea	1.89
Mean high tide in Wadden Sea	1.44	No. of sunshine hours	1.81
Salinity in North Sea	-1.43	Average air temperature at De Kooy	1.56
Porpoise sightings in southern North Sea	14.10	Catches of horse mackerel for NE Atlantic	6.53
Marshland area in Groningen	-7.70	Landing of cod from North Sea catches	-5.50
Abundance of dinoflagellate in southern NS	-5.48	Porpoise sightings in southern North Sea	4.85
Marshland area in Friesland	5.10	No. of harbour seal pups in Wadden Sea	3.48
Recruit number of herring in Marsdiep	4.89	Relative abundance of solenet in NCP	3.22
Abundance of worm-eating waders	-4.12	No. of dark-bellied Brent geese in Western Europe	2.87
No. of dark-bellied Brent geese in western Europe	4.04	No. ha ⁻¹ of scaldfish in NCP	2.72
Landing of plaice from North Sea catches	4.02	No. ha ⁻¹ of lesser weever in NCP	2.52
Winter polychaete biomass	2.80	Landing of haddock from North Sea catches	-2.42
Landing of whiting from North Sea catches	-2.53	Abundance dinoflagellate in southern North Sea	2.19

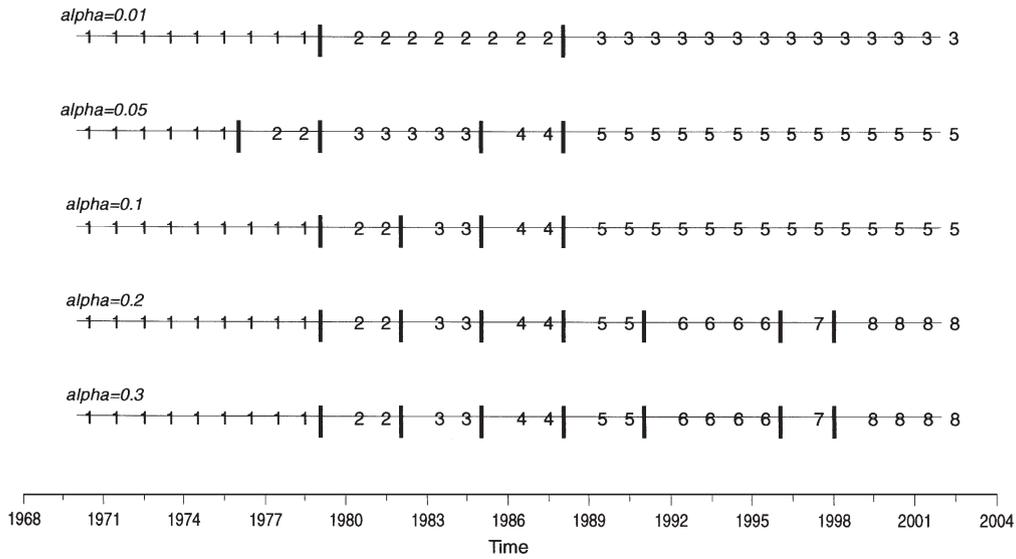


Fig. 10. Results of chronological clustering for the combined biological and environmental variables. Small values of alpha show the most important breakpoints (indicated by vertical lines). Numbers correspond to groups of years

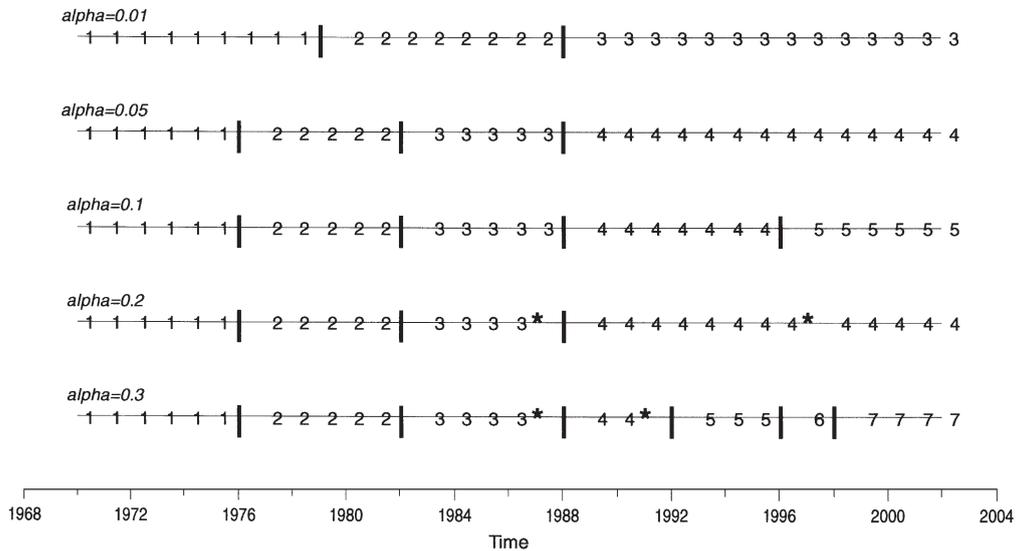


Fig. 11. Results of chronological clustering applied to the biological variables. Small values of alpha show the most important breakpoints (indicated by vertical lines). Numbers correspond to groups of years. *: 'singletons', years that do not belong to the group immediately before or after them and were thus omitted from the calculations

and 1988 were identified as the most important breakpoints. Note that for larger alpha values, 1988 was still identified as a breakpoint, but not 1979. This means that overall, 1979 was a major breakpoint but, when considered on a smaller scale, the years around 1979 differed also.

The asterisks in Fig. 11 are so-called 'singletons', years that do not belong to the group immediately before or after them. As such they were omitted from the calculations (Legendre et al. 1985). It can be con-

cluded that 1979 and (especially) 1988 comprised major breakpoints in the biological data.

Environmental data

Finally, the results of chronological clustering applied to the environmental variables are presented in Fig. 12. The results revealed 1977 and 1989 as the major breakpoints for the environmental data. It is

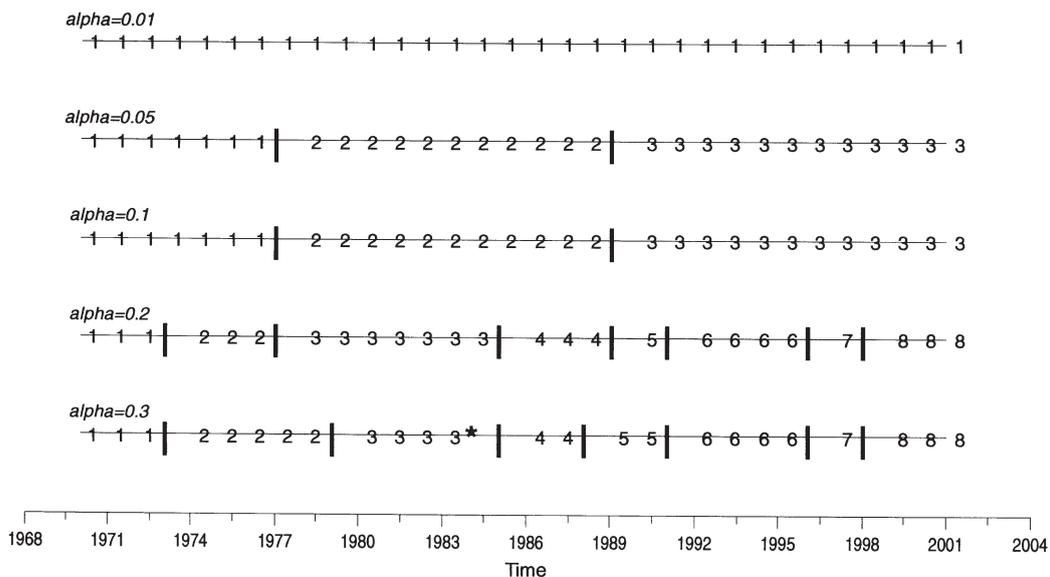


Fig. 12. Results of chronological clustering applied to the environmental variables. Small values of alpha show the most important breakpoints (indicated by vertical lines). Numbers correspond to groups of years. *: 'singletons', years that do not belong to the group immediately before or after them and were thus omitted from the calculations

interesting that for $\alpha = 0.01$ the algorithm identified all years as 1 group, meaning that the grouping appears at a slightly more detailed level.

DISCUSSION

Following the approach of Hare & Mantua (2000), we identified possible regime shifts in the North Sea/Wadden Sea ecosystem in 1979 and 1988. Firstly, we substantiated those apparent shifts using principal component analysis (PCA). PCA is an appropriate technique if linearity can be assumed (McCune & Grace 2002). To linearize the relationships, we log-transformed the biotic variables. Linearity can be checked in various ways, for example by pairplots or scatterplots, or by using coenoclines (Gauch 1982). The latter tool is applied as follows: (1) Apply PCA and extract the components. (2) Calculate smoothing curves for each species along each component. The smoothing curves along a PC are called 'coenoclines' (Gauch 1982). If the smoothing curves are approximately linear, then the relationships are approximately linear and PCA should be used instead of correspondence analysis or detrended correspondence analysis (Jongman et al. 1995). The software package Brodgar (available at: www.brodgar.com) automatically calculates these coenoclines, and the results for our data indicated that relationships were indeed approximately linear. This is also confirmed by the results of our initial data exploration using pairplots and scatterplots.

Secondly, we employed the regime shift analysis (RSA) of Ebbesmeyer et al. (1991) to corroborate the timing of the shifts. By its nature, PCA requires a large element of subjective interpretation, but our results are certainly highly consistent with the idea that meaningful regime shifts occurred in the late 1970s (1978 or 1979) and late 1980s (1988 or 1989).

Thirdly, because of the ongoing discussion as to whether RSA is an appropriate statistical technique to identify breakpoints, we also applied chronological clustering. The results obtained by this method confirmed the results of RSA and PCA. We even applied a 4th statistical technique, namely discriminant analysis (DA). The results are not presented here, but they indicated a statistical significant difference (when assuming normality) between the interactions of the variables in the 3 time periods: 1970 to 1979, 1980 to 1988 and 1989 to 1997. When the normality assumption does not hold, then DA still shows separation of the 3 regimes, although the word 'significant' can no longer be used.

Thus, based on 4 different statistical techniques, we found strong evidence of regime changes in 1979 and 1988, although the exact timing of the breakpoints is not clear-cut. Causal relations and hence the nature of the changes could not be determined by the methods used, but it is possible to conclude which variables are most strongly related to the patterns observed.

The 2 apparent regime shifts were both upwards, i.e. the second shift in 1988 did not return the ecosystem to the pre-1979 situation, but changed it again by an

overall increase in mean annual values. Therefore, there appears to have been an overall upwards trend in environmental and ecological variables largely determined by 2 sudden upward shifts. Considering the contribution of all variables to the 2 regime shifts (Fig. 9), it is clear that the shift was not caused by a certain identifiable subset of variables; on the other hand, not all variables contributed to the steps (some variables had values close to zero). Furthermore, it is obvious that predominantly biological time series contributed to the larger average step-magnitude. These results suggest that feedbacks such as nutrient availability or selective grazing could be stabilizing the community in a certain state; but are environmental events the trigger? To answer this we need to examine the data in more detail.

Regime shift in 1979

Environmental variables

The solar constant showed the greatest difference in the 1979 shift of the environmental variables (Table 4). The reconstructed solar constant (<http://climexp.knmi.nl/>) exhibited an oscillating pattern with cycles of ~11 yr (comparable with the sunspot cycle), and a gradual increase in values since 1900. Apart from the probable anthropogenic causes for increases in global temperature, the amount of solar irradiance may also be a contributing factor: when the solar constant cycle is in its increasing phase, it may trigger changes in other climate indices as well, with the overall effect of a large-scale drastic environmental alteration. The influence of the sun (sunspot/solar constant) has been controversial since the early 1990s, when 2 Danish researchers showed a direct relationship between sunspot number and global temperature (Friischristensen & Lassen 1991). The role of the sun in the earth's climate remains the subject of much debate (Pap et al. 2002, Rind 2002, Solanki 2002). Our results suggest that changes in the solar constant were a factor in both ecosystem shifts, albeit its influence appeared to be much less in the 1988 shift.

The second highest difference in the 1979 regime shift was in the East Atlantic (EA) teleconnection pattern, measured in all but the summer (June, July, August) months. This EA pattern is similar to that of the North Atlantic Oscillation (NAO), except that the pressure locations are more southeasterly compared with the NAO. In addition, the lower latitude-anomaly centre contains a strong subtropical link, reflecting large-scale modulations in the strength and location of the subtropical ridge. As for the NAO, the EA pattern entered a positive phase in the late 1970s/early 1980s.

Boberg & Lundstedt (2002) proposed a relationship between solar wind and the large-scale pressure system in the North Atlantic. This relation could be reflected in the shift in the EA pattern in 1979.

The mean high tide in the Wadden Sea also showed a large step-magnitude in 1979, possibly influenced by an increase in wind speed (Dijkema 1997). This could be related to the atmospheric pressure change which, in turn, could be related to solar wind (Boberg & Lundstedt 2002). The high step-magnitudes found in the salinity of the North Sea and Wadden Sea are obviously related to the great salinity anomaly which entered the North Sea in 1977 and 1978 (Lindeboom et al. 1995).

Biological variables

Apart from increased porpoise sightings, a striking phenomenon of the first regime shift was a change in phytoplankton composition. For example, the dinoflagellate *Ceratium macroceros* was absent from continuous plankton recorder surveys after 1979. Edwards et al. (2002) related this to the salinity anomaly. Simultaneously, the abundance of polychaetes in the western Wadden Sea suddenly increased (Beukema et al. 2002). There was a steep decline in the landing of whiting, possibly coupled to a change in composition of the Atlantic water mass entering the North Sea, while the landing of plaice and the number of recruits of herring increased. In turn, it is likely that a change in the abundance of polychaetes and fish species led to a change in the abundance of worm-eating waders and porpoises, respectively. Coinciding with this was an increase in the number of dark-bellied Brent geese in the whole of western Europe. The biological variables showing a sudden change were not limited either geographically or to any particular trophic level, and therefore support the large-scale regime shift hypothesis.

Regime shift in 1988

Environmental variables

The physical variables that showed the greatest step-magnitude in 1988 were all temperature related, indicating a possible relationship between climate and this regime shift. Superimposed on global warming, sudden jumps apparently occurred, which can also be seen in the original time series. The solar constant cycle reached a new minimum in 1987. The subsequent increase could partly have triggered the jump seen in the climate indices. Also coinciding with this

was the change in the winter NAO index, which increased from 1988 onwards to its highest positive level observed in the 20th century. This resulted in an increased inflow of relatively warm Atlantic water, leading to warm sea-surface temperature and high salinity and possibly also increased nutrient inflow. It has been estimated that 90% of the nutrients (P, N) in the North Sea come from the North Atlantic (Edwards et al. 2002). In turn, these sudden changes will have affected the marine ecosystems and thus the biological variables.

Biological variables

Several fish species showed dramatic changes in abundance, evident in records of non-commercial species like solenet and scald fish and of landings of cod and haddock. Once again the abundance of the dinoflagellate *Ceratium macroceros* also changed, but this time it increased. Similar to the 1979 shift was the increase in porpoise sightings and the number of Brent geese. Additionally, the relative number of harbour seal pups increased.

Not all variables showed a change coinciding with the 2 regime shifts (see Table 1), e.g. the winter temperature of the Wadden Sea and the landing of sole showed no change during the 1979 shift, while during the 1988 shift, the EA teleconnection pattern, the winter abundance of gastropods, the yield of Norway pout and the seal strandings did not change at all. However, a vast majority of the data series available for this analysis indicated major shifts.

CONCLUSIONS

For both shifts, environmental variables seemed to trigger a change without themselves displaying a very clear change (e.g. Fig. 8), whereas the biological variables seemed to maintain the situation in a new stable state. These patterns are reflected in the great resemblance between the PC scores of the biological time series only and of all variables combined, and the low year-to-year variability in the biological data sets. However, it should be kept in mind that all time series made an equal contribution to the calculations and that we had twice as many biological time series as environmental time series.

To summarise possible environmental triggers of the shifts of 1979 and 1988, the first seemed to be related to salinity and possibly weather conditions, whereas the second could be related to weather and, more specifically, temperature. Therefore, it appears possible that ocean climate conditions have had far-reaching conse-

quences on the ecology of the North Sea, but at present it is not possible to say what the primary cause(s) of these conspicuous ecosystem shifts were. Lindeboom (in press) hypothesizes that there may be a combination of factors, a complex interaction between ocean, climate, anthropogenic perturbations and atmospheric oscillations, each having a varying degree of importance. The spatial and temporal scales of measured variables play an important role in the types of shifts they can reflect. Variables that have the ability to respond instantly, such as phytoplankton, temperature and spatial distribution of larger organisms, can show sudden jumps while changes in other variables, such as age distributions, biomass and abundance of larger organisms, are reflected more by a lag phase or by longer-term trends.

Our results indicated a number of patterns similar to Hare & Mantua's (2000) study of the North Pacific, including an overall trend with sudden changes superimposed, and that those state-shifts are reflected more consistently by biological time series rather than by physical indices. However, certain differences were found between the 2 studies, including the years of change and the importance of the climate indices. In the North Pacific, the first regime shift apparently took place in 1977, and the second in 1989, whereas we found that the biggest changes in North Sea and Wadden Sea took place in 1979 and 1988. In the North Pacific, the 1977 regime shift was apparently triggered by climate indices, whereas we found the influence of these factors to be stronger in the 1988 shift. The great similarity between the 2 studies, however, could indicate that the climate-ocean interaction, including marine biological processes, changed in the whole of the temperate Northern Hemisphere with a lag phase in NW Europe in the first regime shift and a lag-phase in the North Pacific in the second regime shift. The occurrence of jumps has also been found in other ecosystems. Scheffer et al. (2001) found that gradual changes in the ecosystems of lakes, coral reefs, forests and arid lands can be interrupted by sudden drastic switches to contrasting states. The fact that the observed regime shifts occurred more or less simultaneously in both the North Sea and Wadden Sea, and in the North Pacific, supports the hypothesis of some common causes, such as ocean-climate changes. It is obvious that physical indices have a large influence, but this influence requires further research if it is to become predictable.

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