

A long-term chlorophyll data set reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient trends

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Abstract

During the 1980s, a rapid increase in the Phytoplankton Colour Index (PCI), a semiquantitative visual estimate of algal biomass, was observed in the North Sea as part of a regionwide regime shift. Two new data sets created from the relationship between the PCI and SeaWiFS chlorophyll *a* (Chl *a*) quantify differences in the previous and current regimes for both the anthropogenically affected coastal North Sea and the comparatively unaffected open North Sea. The new regime maintains a 13% higher Chl *a* concentration in the open North Sea and a 21% higher concentration in coastal North Sea waters. However, the current regime has lower total nitrogen and total phosphorus concentrations than the previous regime, although the molar N:P ratio in coastal waters is now well above the Redfield ratio and continually increasing. Besides becoming warmer, North Sea waters are also becoming clearer (i.e., less turbid), thereby allowing the normally light-limited coastal phytoplankton to more effectively utilize lower concentrations of nutrients. Linear regression analyses indicate that winter Secchi depth and sea surface temperature are the most important predictors of coastal Chl *a*, while Atlantic inflow is the best predictor of open Chl *a*; nutrient concentrations are not a significant predictor in either model. Thus, despite decreasing nutrient concentrations, Chl *a* continues to increase, suggesting that climatic variability and water transparency may be more important than nutrient concentrations to phytoplankton production at the scale of this study.

Phytoplankton are the primary producers of pelagic marine waters, the base of the marine food web, and thus an integral part of the ecosystem, affecting trophic

dynamics, nutrient cycling, habitat condition, and fishery resources (Paerl et al. 2003). Additionally, plankton are closely coupled to environmental change (Hays et al. 2005), making them sensitive indicators of environmental disturbance.

Between 1983 and 1988, a rapid change occurred in many biological and ecosystem processes and individual species in the North Atlantic region (Beaugrand 2004). A shift in the proportion of cold and warm water species of *Calanus* (Reid et al. 2003), phenological changes in production resulting in trophic mismatch (Edwards and Richardson 2004), an influx of oceanic species (Lindley et al. 1990), and changes in zooplankton community structure and salmon abundance (Beaugrand and Reid 2003)

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occurred in the North Sea during the mid- to late 1980s. Additionally, phytoplankton production demonstrated a marked increase across the North Atlantic and North Sea regions during that period (Reid *et al.* 1998; Edwards *et al.* 2001). These changes, observable across multiple trophic levels, are linked to what has been described as a regime shift, a stepwise alteration in the composition and productivity of the whole ecosystem at a regional scale that reflects major hydrographic change (Reid *et al.* 2001a; Beaugrand 2004).

In part, the cause of the late 1980s North Sea regime shift may have been a response to a switch in the behavior of the winter North Atlantic Oscillation (NAO) from a negative phase to its longest ever positive phase (Beaugrand 2004; Alheit *et al.* 2005; Weijerman *et al.* 2005). A positive phase NAO influences the North Sea ecosystem through regional climate effects including increased sea surface temperature, strong westerly winds (Beaugrand 2004; Alheit *et al.* 2005; Weijerman *et al.* 2005), and increased inflow of warm, salty water from the Atlantic Ocean (Edwards *et al.* 2001; Reid *et al.* 2003; Beaugrand 2004).

Although oceanic algal production is an important component of the marine system, few long-term biological data sets exist for European waters. The lack of time-series data has made it difficult to identify trends in phytoplankton production dynamics and establish linkages to natural variability or anthropogenic change (Edwards *et al.* 2001). The Continuous Plankton Recorder (CPR) survey, an upper-layer plankton monitoring program operated since 1931, provides the only long-term biological plankton data set with spatial coverage across coastal and open North Sea waters (Edwards *et al.* 2001). The first level of analysis the CPR offers is the Phytoplankton Colour Index (PCI), a semiquantitative *in situ* measurement of phytoplankton biomass (see Methods section). The PCI was recently used in conjunction with phytoplankton chlorophyll *a* (Chl *a*) data estimated by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite to extrapolate a new 50-yr Chl *a* data set for the Northeast Atlantic and North Sea (Raitos *et al.* 2005).

As an area rich in natural resources, much of the North Sea has been affected by anthropogenic impacts including fishing, nutrient runoff, and oil, gas, and aggregate extraction (Clark and Frid 2001). Because of its proximity to land, the degree of impact on the coastal area is likely to be greater than that affecting the open North Sea. The aim of this paper is to separately extrapolate the SeaWiFS data set back 50 yr for the open and coastal North Sea in order to assess the long-term variability of Chl *a* within and between these two regions and to relate the Chl *a* time series to environmental and climatic variation. In this paper, an attempt is made to explain trends observed in phytoplankton biomass based on environmental, climatic, and nutrient related factors and processes. The biological, environmental, and climatic differences between the pre- and post-regime shift North Sea system were also examined, and factors generating change were investigated, including nutrient concentrations, water transparency, sea surface temperature (SST), sea-level pressure (SLP), precipitation, wind stress, and climatic variability.

Methods and materials

Area of study—The North Sea is bordered by some of the most densely populated and highly industrialized Western European countries; its catchment covers an area of 850,000 km² and contains 184 million people (OSPAR Commission 2000). The North Sea has been a productive fishing ground and is heavily exploited for oil, gas, and aggregates. Additionally, the North Sea is extensively used for transport as well as for the dumping of dredged material. From an environmental perspective, the North Sea is an ecologically rich and diverse environment; a number of endangered species and important habitats, some of which are now protected, are found within the North Sea ecosystem (OSPAR Commission 2000).

For the purpose of this study, the limit of the coastal North Sea was defined as a standard 30-nm (56-km) distance from land (Fig. 1). In order to minimize the impact of land-based activities, the open North Sea was designated as the area greater than 125 nm (231 km) from the shore. Polygons representing the open and coastal North Sea study areas were constructed with ESRI ArcMap 9.0. These polygons were used to select the corresponding data points for each geographically referenced data set used in this analysis (PCI, SeaWiFS, PCI–SeaWiFS matchups, SST, sea-level pressure, wind stress, precipitation, nutrient concentrations, and transparency measurements).

Data extraction

Environmental data—Annual surface (top 10 m of water column) nutrient concentration data for the North Sea and Elbe and Rhine rivers were obtained from the European Environment Agency's Waterbase (EEA) via their Web site (<http://dataservice.eea.eu.int/dataservice/>). Waterbase contains reliable and validated data collected from the national monitoring programs of the member countries of the EEA and therefore comprehensively covers a large geographical area, a requirement that is paramount to our study. To assess variability of nutrient input, Elbe and Rhine river discharge data were obtained from the Global Runoff Data Centre, a digital worldwide repository of discharge data and associated metadata (Global Runoff Data Centre 2005).

Coastal water transparency data were extracted from the Secchi Disk Data Collection for the North Sea and Baltic Sea (available at <http://www.ices.dk/ocean/project/secchi/>) compiled by Thorkild Aarup (Aarup 2002). While the transparency data set contains a considerable number of samples ($n = 5,057$) with a wide spatial and temporal resolution, they are not uniformly distributed in time or space. Temporally, the 1990s was the most heavily sampled decade ($n = 3,056$) followed by the 1980s ($n = 1,188$) and the 1970s ($n = 758$); thus, the accuracy of trend in Secchi depth increases with time. The majority of samples were taken in the Dutch, German, Danish, and Norwegian waters of the southern North Sea ($n = 2,730$) and Skagerrak ($n = 2,116$). The remaining samples are from the coastal areas of the United Kingdom and western

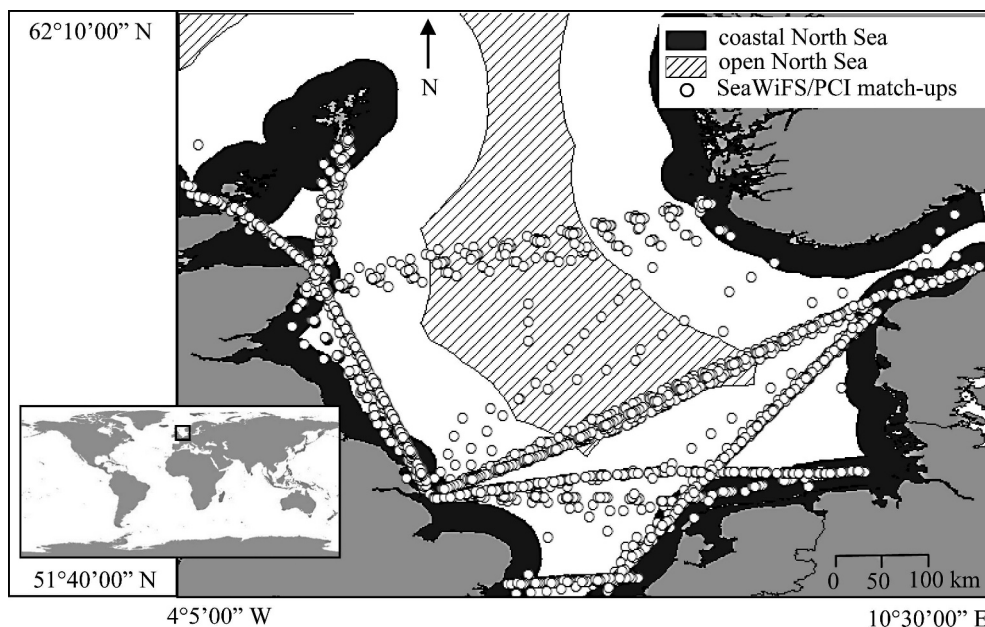


Fig. 1. Location of coastal and open North Sea areas used in study overlain by CPR samples temporally corresponding with SeaWiFS chlorophyll measurements ($n = 3,695$).

Norway. Water transparency is dependent on phytoplankton biomass, dissolved particulate organic matter, suspended sediments, and yellow substances in the water column (Sanden and Hakansson 1996) as well as water column stability.

The NAO is an important index of climatic variability affecting the North Sea and influences its ecology through SST, wind direction and magnitude, and precipitation (Ottersen et al. 2001) and is strongly linked to oceanic inflow into the North Sea (Reid et al. 2003). The winter (December–March) NAO index (NAOI) was acquired from the Web site of Jim Hurrell at the National Center for Atmospheric Research. The NAOI is based on the difference in normalized sea-level pressure between Lisbon, Portugal, and Stykkisholmur, Iceland (Hurrell 1995). Mean annual SST data were obtained from the Hadley Center, UK Met Office (HadSST v1.1). Monthly mean precipitable water content (as a measure of precipitation) and sea-level pressure data were obtained from the NCEP/NCAR Reanalysis Project at the NOAA-CIRES Climate Diagnostics Center (<http://www.cdc.noaa.gov/cdc/reanalysis/>). Wind speed data, also obtained from the NCEP/NCAR Reanalysis Project, were converted into wind stress data. Wind stress is a function of wind speed, nondimensional drag coefficient, and boundary layer air density (Pickard and Pond 1978). Wind stress regulates the dynamics of the boundary layer and is connected to the production of wind-driven surface currents, the generation of surface waves, and upper-ocean mixing (Pickard and Pond 1978). Therefore, low wind stress is associated with highly stratified waters.

Data on the influx of Atlantic waters entering the North Sea between the Orkney Islands and Utsira were obtained from the NORWECOM 3-D hydrodynamic model (Iversen

et al. 2002). Model generated data were used, as no long-term measured time series exist.

Primary production data—PCI data were extracted from the CPR database for the North Sea. During the period 1948–2003, the CPR survey collected approximately 52,000 samples. Although the CPR has been sampling in the North Sea since 1931, data from 1948 onward were used as the methodology of sampling, and measurement of PCI has remained consistent since 1948 (Batten et al. 2003a). Samples are collected by a high-speed plankton recorder (~15–20 knots [28–37 km h⁻¹]) that is towed behind “ships of opportunity” in the surface layer of the ocean (~10 m depth); one sample represents 18 km of tow. Accumulation of phytoplankton cells on the silk gives it a greenish color (Batten et al. 2003b); the PCI is based on a relative scale of greenness and determined on the silk by reference to a standard color chart. There are four different “greenness” values: 0 (no greenness), 1 (very pale green), 2 (pale green), and 6.5 (green). Categories of PCI are assigned numerical values based on acetone extracts (Colebrook and Robinson 1965). PCI is a unique measurement of phytoplankton biomass, as small phytoplankton cells that cannot be counted under the microscope contribute to the coloration of the filtering silk (Batten et al. 2003b).

SeaWiFS current reprocessed version (v5.1) data produced by Ocean Biology Processing Group were acquired from the NASA Ocean Color Web site (<http://oceancolor.gsfc.nasa.gov/>). The data were level 3, 8-d products (9 × 9 km⁻² square resolution) of the near-surface Chl *a* concentration (mg m⁻³), estimated using the ocean Chlorophyll 4—version 4 (OC4-v4) algorithm (O’Reilly et al. 1998):

$$\text{Chl } a = 10^{(0.366 - 3.067x + 1.930x^2 + 0.649x^3 - 1.532x^4)},$$

where $x = \log_{10}((R_{rs,443} > R_{rs,490} > R_{rs,510})/R_{rs,555})$ and R_{rs} is the satellite-calculated remote sensing reflectance. The first (x) equation takes the highest reflectance value from a waveband at 443, 490, or 510 nm and divides it by the reflectance at 555 nm; reflectance maximum moves toward higher wave bands as the Chl *a* concentration increases. This x value then goes into an equation that results from a statistical fit of this empirical algorithm to a large in situ database.

NASA processed these data using a series of radiometric corrections (e.g., atmospheric) to eliminate the presence of clouds, haze, and water vapor (Mueller and Austin 1995). The 8-d data products were used in order to increase the number of CPR–SeaWiFS matchups, as the daily data were highly obscured by cloud cover.

Data analysis

Matching SeaWiFS and PCI data—Seventy-six months (September 1997–December 2003) of in situ measurements of PCI and satellite Chl *a* values were compared for the North Sea. Concurrent SeaWiFS and CPR measurements were collated for the same spatial and temporal coverage. Then, refining the technique developed and used on a larger scale by Raitsos et al. (2005), coastal and open North Sea samples were selected based on the areas shown in Fig. 1. The finer geographical scale helped us establish more accurate relationships between the PCI and SeaWiFS Chl *a* for the open and coastal North Sea study areas. In the North Sea, the CPR survey collected 6,294 different samples for the 6-yr period, 2,311 of which fell within 30 nm (56 km) of the coast and 723 of which were located in the defined open North Sea area. After screening the SeaWiFS data set for CPR matchups, 1,272 samples could be used for comparison in the coastal North Sea (44.96% of coastal data did not have a SeaWiFS matchup, primarily because of cloud coverage), and only 412 could be used in the open North Sea. As we considered 412 too small a sample size to establish a reliable relationship, all available noncoastal North Sea matchups (3,695) were used to construct the relationship to be applied to the open North Sea (Fig. 1). PCI data are on a ratio scale (i.e., not only can PCI categories be ranked, but differences are quantified). Thus, Pearson correlation (or linear regression) is appropriate to assess the strength of the relationship between SeaWiFS and PCI data (Zar 1984; Raitsos et al. 2005). SeaWiFS data were log-transformed to improve homogeneity of variance and normality (Zar 1984).

The PCI and SeaWiFS data sets demonstrate an overall increase in chlorophyll during the study period. Highly significant positive relationships exist between PCI and SeaWiFS data for the entire North Sea ($r = 0.26$, $p < 0.001$) and for the coastal area ($r = 0.30$, $p < 0.001$). As these relationships are nonlinear, the mean SeaWiFS Chl *a* value was calculated for each PCI category in each North Sea region (Fig. 2). Using the significant relationships between PCI and SeaWiFS Chl *a* for each region (Fig. 2) and the total number of CPR samples analyzed (approximately 52,000) for the period 1948–2003, retrospective

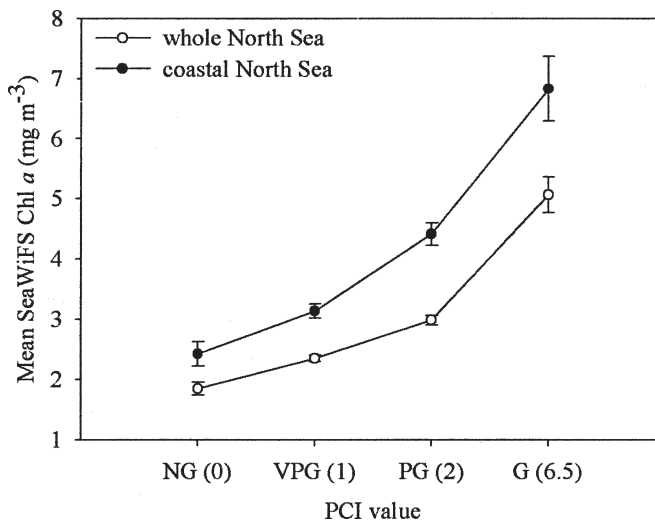


Fig. 2. Equivalent SeaWiFS–PCI values for whole and coastal North Sea areas with 95% confident limits. This relationship was applied to the PCI data set to extrapolate the new Chl *a* time series. The PCI is a ratio scale of phytoplankton color with four “greenness” values: 0 (NG = no greenness), 1 (VPG = very pale green), 2 (PG = pale green), and 6.5 (G = green). Note there is no overlap between confidence intervals for each PCI category.

calculations of Chl *a* for the coastal and open North Sea could be produced.

Simple correlation analysis (Pearson) and multiple linear regression were used to determine the existence and strength of possible relationships between environmental and biological variables. For multiple regression modeling, data were first assessed for normality (Kolmogorov–Smirnov test) and transformed if necessary. Models were estimated using forward selection stepwise regression procedures with Chl *a* (coastal or open) as the dependent variable and a suite of environmental parameters as candidate independent variables. Robustness of resulting models (α set at 0.05) was assessed by testing the residuals for normality (Kolmogorov–Smirnov test) and homoscedasticity (scrutinizing plots of standardized residuals). All significant analyses conformed to these regression assumptions. Standardized regression coefficients were used to infer the relative importance of model variables for explaining variations in Chl *a* data.

Potential biases—Consistency and comparability of the methodology used in the CPR survey has been studied in depth (Batten et al. 2003a). Although standard methods have been used for more than 50 yr in the survey, the PCI has been measured by a number of different analysts during this time. However, evaluating greenness is a simple task that is typically undertaken by two or three people in a year, many of whom have done this work for more than a decade. As well as referring to a standard color chart, apprentices are trained in assessing PCI for a year before performing the task on their own (Raitsos et al. 2005).

The study area includes both Case I (open ocean) and Case II (optically complex coastal) waters (International Ocean-Color Coordinating Group [IOCCG] 2000). In Case

II waters, Chl *a* is difficult to distinguish from particulate matter and/or yellow substances (dissolved organic matter), and so global chlorophyll algorithms (such as OC4-v4) are less reliable (IOCCG 2000). Previous work applying the PCI/SeaWiFS Chl *a* relationship has occurred primarily in Case I waters (Raitso et al. 2005). This is the first time the relationship has been used to create a Chl *a* time series for a substantial geographic area featuring optically complex Case II waters; this analysis is possible because of the coupling between remotely sensed (SeaWiFS) and in situ (PCI) measurements.

Results

Environmental measures—Since 1958, annual mean SST in the North Sea has demonstrated an increasing trend that was most pronounced during the late 1980s and continues through to the present (Fig. 3) (Edwards et al. 2002). Across the North Sea, mean SST increased by 0.48°C between the 1960s and 1990s; locally, the increase was greatest in the southern North Sea waters (0.75°C) and least in the northern North Sea (0.18°C). The increasing trend in SST is related to changes in the NAO (Ottersen et al. 2001) and is also highly correlated with Northern Hemisphere temperature (Beaugrand and Reid 2003). During the 1950s and 1960s, the NAO was in a negative phase, but from 1972 to 2002, it was in its longest ever positive phase, reaching its highest recorded value in 1989. The phytoplankton growing season has been lengthened by the resulting warmer SST in the North Sea (Reid et al. 1998).

Secchi depth data ($n = 5,057$) showed that, after a major decline during the early 1970s, water transparency in coastal North Sea waters has been increasing (Fig. 3). Improvement during both summer and winter has been greatest since the mid-1970s, with a mean summer Secchi depth of 2.6 m and a mean winter depth of 1.8 m during the 1975–1979 period in contrast to a summer mean of 6.1 m and a winter mean of 5.7 m between 1991 and 1995.

Inflow of oceanic waters to the North Sea from the Atlantic Ocean displayed an increase throughout the 1960s and early 1970s before decreasing from 1976 through 1980 (Fig. 3). During the early and mid-1980s, inflow continued to increase, reaching a maximum volume of more than 2.5 standard deviations above the long-term mean in 1989. From 1988 to 1995, influx of Atlantic waters remained consistently above the long-term mean, although volume of inflow began to decline in 1990. Inflow is significantly positively correlated with the NAOI ($r = 0.63$, $p < 0.001$) and SST ($r = 0.32$, $p = 0.035$) as well as significantly negatively correlated with Rhine ($r = -0.32$, $p = 0.03$) and Elbe ($r = -0.42$, $p < 0.001$) river discharge (Table 1 displays full details of correlation results).

Until 1974, wind stress in the North Sea was predominantly below average for the study period (Fig. 3). After 1974, wind stress began to show an increasing trend and reached its highest value in 1990. Although, like Secchi depth, wind stress displays an overall increasing trend throughout the late 1970s and 1980s, only a weak negative relationship exists between the two variables (see Table 1).

Wind stress is, however, strongly correlated with Atlantic inflow ($r = 0.70$, $p < 0.001$) and NAOI ($r = 0.64$, $p < 0.001$) but not with SST or precipitation.

Unlike SST, NAO, wind stress, Atlantic inflow, and Secchi depth, precipitation did not show an increasing trend during the 1980s but instead showed considerable variability during that period (Fig. 3). Overall, precipitation was variable during our period of study, with the 1970s being the driest decade and the 1950s the wettest, and showed positive relationships with SST ($r = 0.48$, $p < 0.001$) and summer Secchi depth ($r = 0.43$, $p = 0.02$) but no other environmental variables considered in this study.

Sea-level pressure (SLP) is variable throughout the entire time series (Fig. 3) and is correlated only with winter Secchi depth ($r = 0.47$, $p = 0.03$). There is a more pronounced low-pressure signal at the beginning and end of the series.

Nutrient measures—When examining nutrient data from the North Sea regions, it is clear that the coastal zone was much richer than the open North Sea in total nitrogen (TN) and total phosphorus (TP) (Fig. 4a). Significantly decreasing trends in annual mean TN ($r^2 = 0.65$, $p < 0.001$, $n = 23$) and TP ($r^2 = 0.57$, $p < 0.001$, $n = 23$) were observed in coastal North Sea waters, TN and TP following very similar patterns (but note the difference in scales), with visible peaks in the late 1980s followed by dramatic decreases in TN and TP from 1988 to 2002. These are general trends, observable for nutrients in the coastal North Sea as a whole, and may not reflect local variability. For example, when examined at a finer scale, nutrient concentrations showed a significantly decreasing trend in the Southern Bight area since 1980 (TN: $r^2 = 0.57$, $p < 0.001$, $n = 23$; TP: $r^2 = 0.74$, $p < 0.001$, $n = 23$), but although TP has been decreasing in Norwegian coastal waters ($r^2 = 0.33$, $p < 0.01$, $n = 20$), TN displays an increasing trend in that area ($r^2 = 0.38$, $p = 0.01$, $n = 17$). However, because the concentrations of both TN and TP in the Southern Bight are up to 10 times richer than those in Norwegian coastal waters (data not shown), the general decreasing nutrient trends observable for the coastal North Sea as a whole are heavily weighted by nutrient dynamics occurring in the Southern Bight.

The open North Sea time series of both nutrients have a much narrower range than their coastal counterparts; although the open North Sea lacks adequate data to distinguish any significant trend, there is no indication at all of a temporal change in nutrient levels. As the concentrations of TN and TP decreased in coastal North Sea waters, the molar ratio of N:P rose far above the Redfield ratio of 16:1, the molecular ratio at which diatoms require the two elements (Redfield et al. 1963). The N:P ratio continued to increase in coastal waters (Fig. 4c) with a substantial jump around 1988, while in the open North Sea, N:P remained below the Redfield ratio. Nutrient concentrations in coastal waters are negatively correlated to SST (TN coast: $r = -0.59$, $p < 0.001$; TP coast: $r = -0.53$, $p = 0.01$), while N:P in coastal waters is positively correlated to SST ($r = 0.61$, $p < 0.001$). Possibly because of a lack of sufficient nutrient data, open North

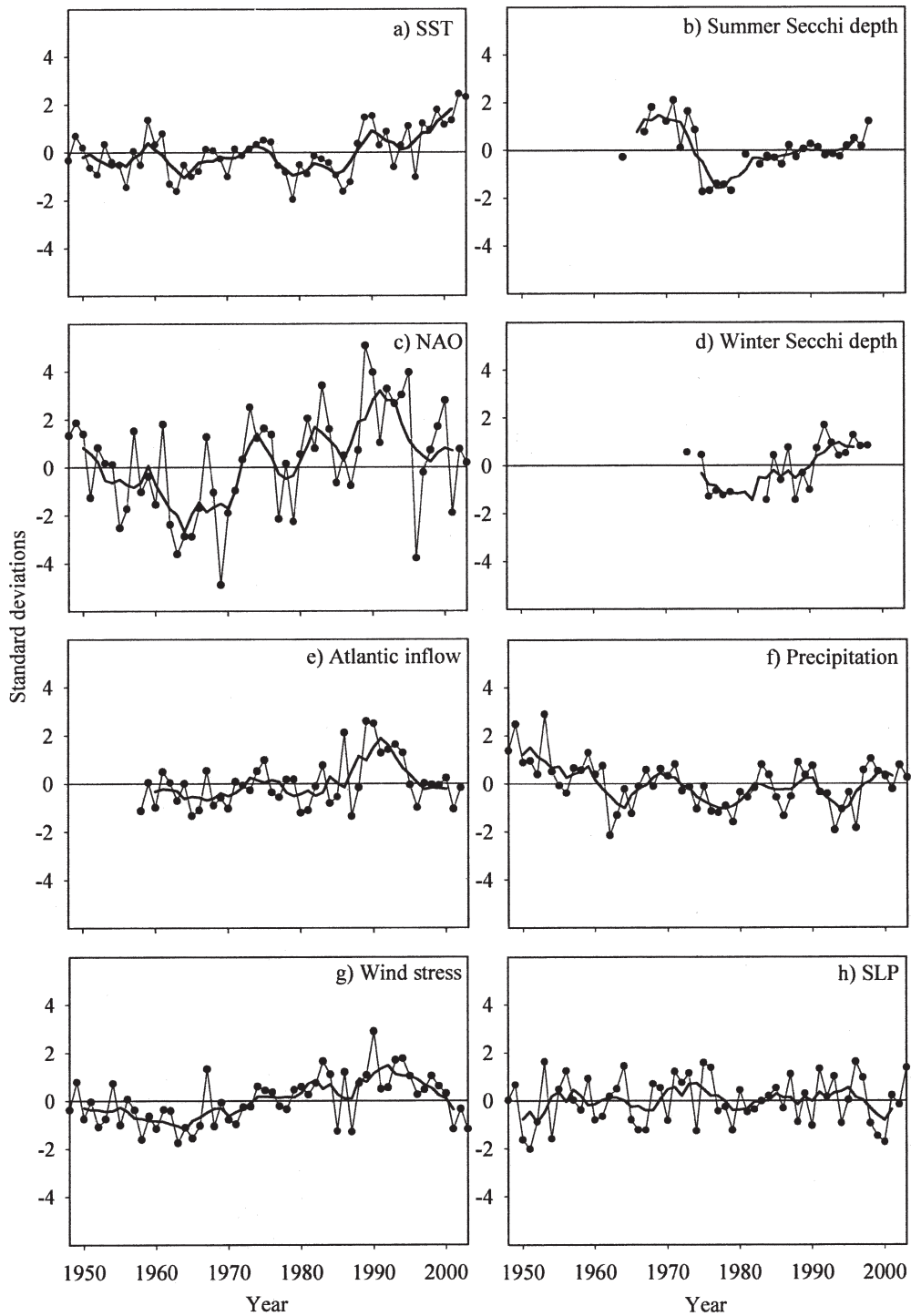


Fig. 3. Time series of (a) SST, (b) summer Secchi depth, (c) NAO, (d) winter Secchi depth, (e) Atlantic inflow, (f) precipitation, (g) wind stress, and (h) SLP with 5-yr running means. With the exception of precipitation (panel f) and sea-level pressure (panel h), all of the environmental variables considered in this study demonstrated a rapidly increasing trend during the 1980s. SST (panel a) and summer (panel b) and winter Secchi depth (panel d) continue to show increasing trends.

Table 1. Results of correlation analysis between the coastal and open Chl a time series and climatic and environmental variables. Significant ($p < 0.05$) results are in bold.

	Chl a open	Chl a coast	TN coast	TP coast	N:P coast	TN open	TP open	N:P open	Elbe flow	Rhine flow	Elbe TN	Elbe TP	Elbe N:P	Rhine TN	Rhine TP	Rhine N:P	Winter NAO	SST	Inflow	Summer Secchi	Winter Secchi	Precipitation	Wind stress	
Chl a coast																								
TN coast	-0.25	-0.65																						
TP coast	-0.08	-0.45	0.80																					
N:P coast	0.07	0.27	-0.63	0.65																				
TN open	-0.16	-0.18	0.51	-0.01	-0.42																			
TP open	-0.09	0.38	-0.22	-0.34	0.03	0.10																		
N:P open	0.00	-0.03	-0.21	0.06	0.34	-0.55	0.05																	
Elbe flow	-0.06	-0.12	0.43	0.59	-0.33	0.12	0.24	0.48																
Rhine flow	0.15	0.12	0.34	0.23	0.06	0.33	0.05	0.35	0.71															
Elbe TN	-0.22	-0.69	0.76	0.73	-0.58	0.22	-0.26	-0.34	0.10	-0.02														
Elbe TP	-0.75	-0.84	0.63	0.56	-0.44	0.12	-0.37	-0.32	-0.21	-0.15	0.93													
Elbe N:P	0.70	0.77	-0.50	-0.41	0.37	-0.18	0.46	0.35	0.43	0.27	-0.79	-0.93												
Rhine TN	0.36	-0.36	0.67	0.68	-0.39	0.19	-0.16	-0.37	-0.14	-0.47	0.90	0.71	-0.46											
Rhine TP	-0.30	-0.77	0.76	0.64	-0.52	0.28	-0.31	-0.28	0.08	0.01	0.97	0.94	-0.82	0.88										
Rhine N:P	-0.29	0.07	-0.55	-0.61	0.27	-0.34	-0.01	0.38	0.26	0.47	-0.72	-0.62	0.48	-0.56	-0.87									
Winter NAO	0.28	0.15	0.13	0.01	0.04	0.00	-0.17	-0.19	-0.16	-0.03	0.11	0.07	-0.11	0.54	0.11	-0.52								
SST	0.32	0.42	-0.59	-0.53	0.61	-0.25	-0.10	-0.08	-0.32	-0.18	-0.62	-0.62	0.54	-0.21	-0.64	0.16	0.50							
Inflow	0.36	0.22	-0.01	-0.12	0.14	0.02	-0.19	-0.34	-0.42	-0.32	0.15	-0.63	-0.59	-0.42	-0.66	0.47	0.63	0.31						
Summer Secchi	0.19	0.35	-0.60	-0.44	-0.09	-0.10	0.11	-0.11	-0.04	-0.06	-0.63	-0.63	0.59	-0.42	-0.66	0.47	-0.03	0.24	-0.16					
Winter Secchi	0.27	0.63	-0.55	-0.48	-0.11	-0.10	0.36	-0.15	-0.17	-0.15	-0.64	-0.58	0.45	-0.72	-0.54	0.19	0.06	0.17	0.02	0.53				
Precipitation	-0.05	-0.09	-0.01	-0.04	0.17	-0.17	-0.49	-0.26	-0.19	-0.21	-0.05	-0.05	0.08	-0.15	-0.10	0.24	0.24	0.48	0.01	0.43	-0.08			
Wind stress	0.30	0.26	0.20	0.05	-0.12	0.28	0.03	-0.38	-0.11	-0.01	0.14	0.09	-0.13	0.67	0.09	-0.57	0.64	0.23	0.70	-0.18	-0.14	-0.02		
SLP	-0.11	0.12	0.07	0.18	-0.29	-0.06	0.32	-0.19	-0.21	-0.40	0.18	0.17	-0.19	0.16	0.14	-0.18	-0.15	0.01	-0.04	0.02	0.47	-0.08	-0.19	

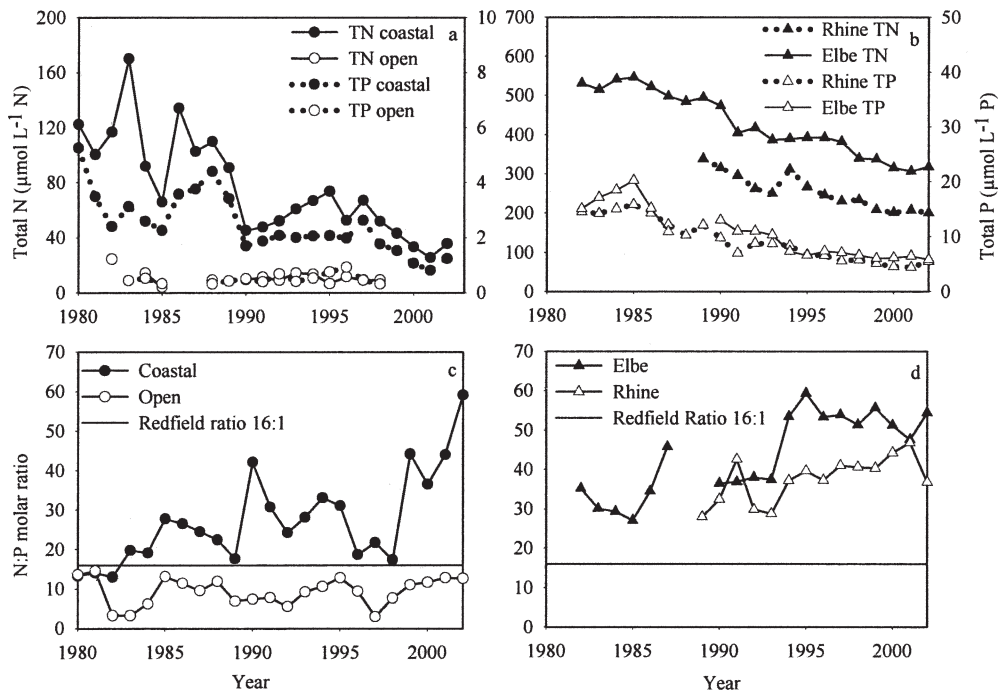


Fig. 4. (a) Annual total nitrogen (TN) and total phosphorus (TP) concentrations in coastal and open North Sea waters and (b) Elbe and Rhine rivers during the period 1980–2002. Both data sets show similar decreasing trends in TN and TP in coastal North Sea and riverine waters despite the differences in scale. As TN and TP concentrations decrease, the molar ratio of N to P is increasing in both (c) coastal North Sea and (d) Elbe and Rhine waters.

Sea nutrients and N:P show no significant relationship with SST or any other environmental variable.

Since the start of our time series in 1982, annual mean nutrient concentrations have decreased in both the Elbe (TN: $r^2 = 0.94$, $p < 0.001$, $n = 21$; TP: $r^2 = 0.71$, $p < 0.001$, $n = 21$) and the Rhine rivers (TN: $r^2 = 0.84$, $p < 0.001$, $n = 14$; TP: $r^2 = 0.91$, $p < 0.001$, $n = 21$) (Fig. 4b). Data from the International Commission on the Protection of the Rhine indicate that Rhine TP has displayed a decreasing trend since 1973 and that Rhine NO_3^- (pre-1982 data on Rhine TN were not available) increased steadily from 1954 before peaking in 1989 and declining thereafter (International Commission for the Protection of the Rhine 2006). Similarly to coastal North Sea waters, the difference in scale between the concentration of TN and that of TP in the Elbe and Rhine rivers has caused an increase in the riverine N:P (Fig. 4d). Concentrations of TN and TP in Elbe and Rhine waters are strongly correlated with coastal North Sea TN (Elbe TN: $r = 0.76$, $p < 0.001$; Rhine TN: $r = 0.67$, $p = 0.009$) and coastal North Sea TP (Elbe TP: $r = 0.56$, $p = 0.012$; Rhine TP: $r = 0.64$, $p = 0.002$) concentrations. Nutrient concentrations in both rivers demonstrate negative relationships with winter Secchi depth (Elbe TN: $r = -0.64$, $p = 0.01$; Elbe TP: $r = -0.58$, $p = 0.04$; Rhine TN: $r = -0.72$, $p = 0.02$; Rhine TP: $r = -0.54$, $p = 0.04$) and summer Secchi depth (Elbe TN: $r = -0.63$, $p = 0.01$; Elbe TP: $r = -0.63$, $p = 0.02$; Rhine TN: $r = -0.42$, $p = 0.23$; Rhine TP: $r = -0.66$, $p = 0.01$). SST is also negatively related to Elbe TN ($r = -0.62$, $p < 0.001$), Elbe TP ($r = -0.62$, $p < 0.001$), Rhine TN ($r =$

-0.21 , $p = 0.47$), and Rhine TP ($r = -0.64$, $p < 0.001$). Note that the correlations between Rhine TN and summer Secchi depth and SST are not statistically significant (Table 1); this may be due to the short time series of Rhine TN (Fig. 4b). Furthermore, data for the Elbe River indicated no significant change in the annual quantity of water discharged into the North Sea between 1948 and 2001, while output from the Rhine increased slightly ($r^2 = 0.09$, $p < 0.05$, $n = 54$) (Fig. 5). Additional analysis also revealed that there has been no seasonal change in discharge pattern for either river. Thus, the absence of change in quantity of river discharge in conjunction with the decline in riverine nutrients indicate that the Elbe and Rhine rivers have reduced their input of these nutrients to North Sea waters.

In general, coastal North Sea and riverine nutrient concentrations have been decreasing since the early 1980s, while open North Sea nutrient concentrations show no clear trend. However, since the early 1980s, SST, Secchi depth, wind stress, and Atlantic inflow have displayed increasing trends, while precipitation and SLP remain variable.

Phytoplankton production measures—The newly created Chl *a* time series shows considerable variability in both the open and coastal North Sea until the mid-1980s when a rapid increase in Chl *a* began to occur (Fig. 6). This increase resulted in a chlorophyll peak in 1989, observable in both the coastal (3.92 mg m^{-3}) and the open (3.15 mg m^{-3}) North Sea. After 1990, the coastal and

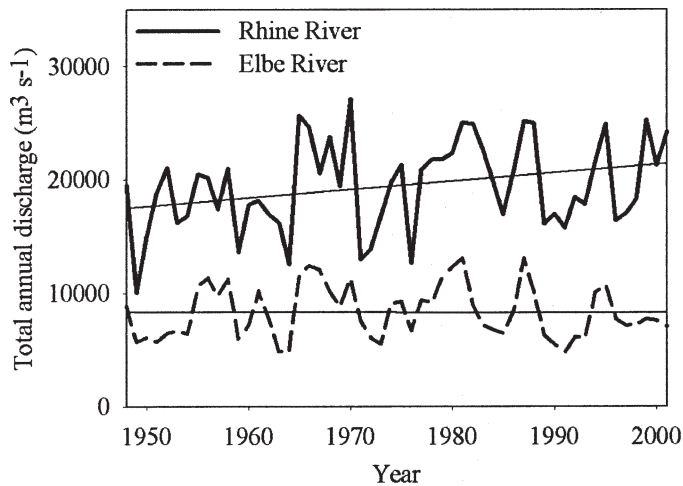


Fig. 5. Annual mean discharge (1948–2001) of Elbe and Rhine rivers. There is no trend in Elbe discharge and a slight increase in Rhine discharge, indicating that the decrease in coastal nutrients can most likely be attributed to the decline in nutrient concentrations in both rivers rather than decreased discharge.

open North Sea have both sustained Chl *a* concentrations well above those maintained before the 1980s rather than returning to pre-phase shift levels (Fig. 6). As mentioned earlier, this pattern of change for the North Sea as a whole has been observed and described as a regime shift (Reid et al. 1998). The changes in Chl *a* observed in coastal waters have occurred throughout the coastal North Sea. The regime shift and subsequent increased level of Chl *a* are visible in the northern ($>58^\circ$ latitude), central (55° – 58° latitude), and southern ($<55^\circ$ latitude) coastal regions of the North Sea (Fig. 7a–c). SST is significantly correlated with both open Chl *a* ($r = 0.32$, $p < 0.05$) and coastal Chl

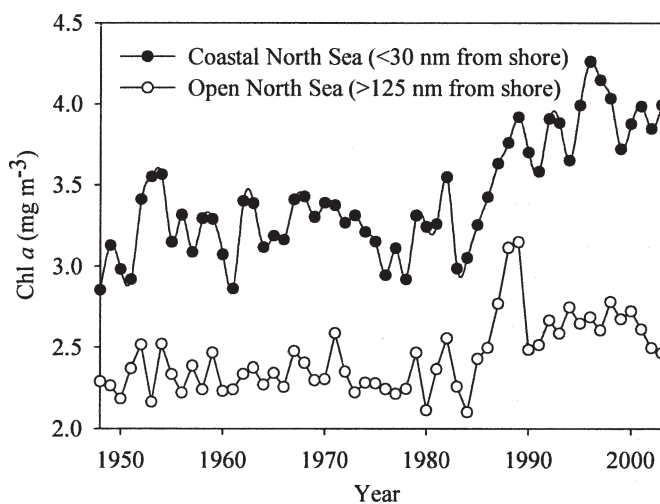


Fig. 6. Time series of the new Chl *a* data set (annual means) for the period 1948 to 2003 in the coastal and open North Sea. The regime shift is evident as a rapid increase in Chl *a* between 1982 and 1989 followed by mean annual Chl *a* concentration that is consistently higher than that observed before the regime shift. Both open and coastal North Sea time series show a higher level of Chl *a* in the period after the regime shift than in the period before.

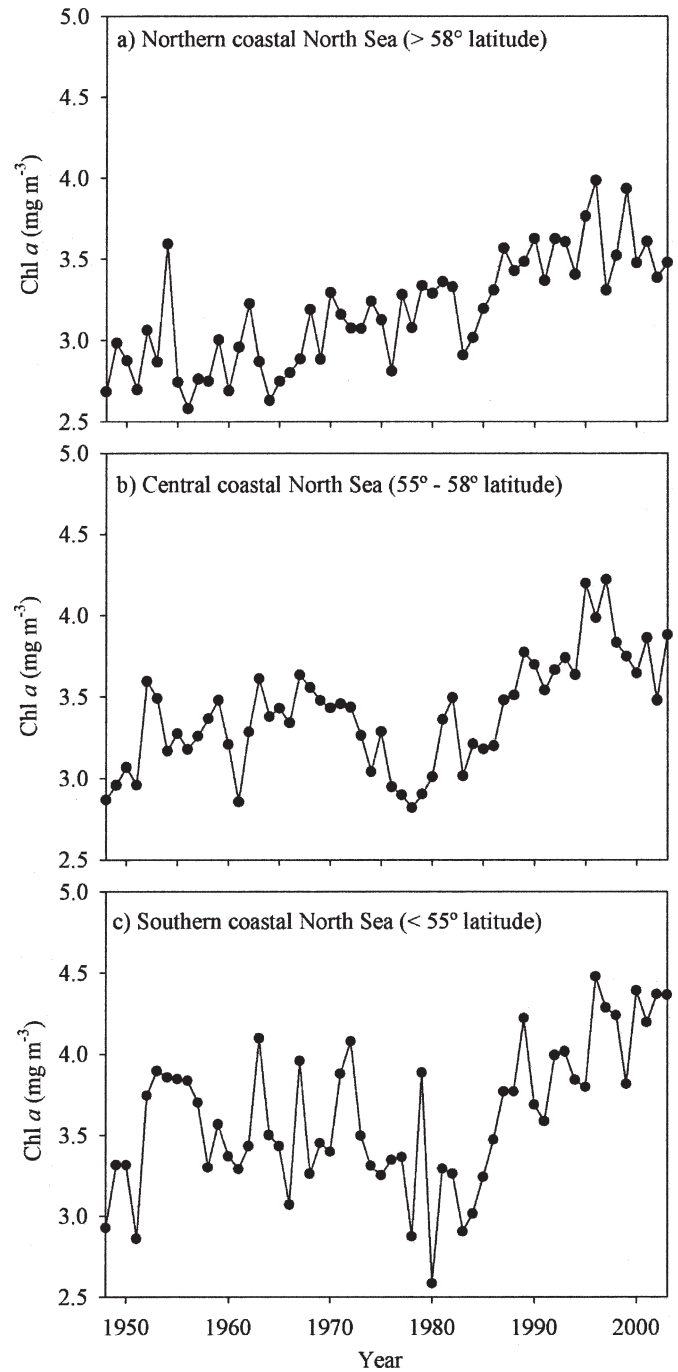


Fig. 7. Trends in Chl *a* in the (a) northern, (b) central, and (c) southern coastal regions of the North Sea.

a ($r = 0.42$, $p < 0.01$). Also, winter NAO is significantly correlated with Chl *a* in the open North Sea ($r = 0.28$, $p = 0.036$) but not with coastal Chl *a*. Wind stress, however, is significantly positively correlated with both open Chl *a* ($r = 0.30$, $p = 0.03$) and coastal Chl *a* ($r = 0.26$, $p = 0.05$). Coastal Chl *a* also has a strong significant relationship with winter Secchi depth ($r = 0.63$, $p = 0.002$), while open Chl *a* is positively correlated with Atlantic inflow ($r = 0.36$, $p = 0.01$). Most interestingly, coastal Chl *a* was found to have a significant negative relationship with both TN ($r =$

Table 2. Results of multiple linear regression analyses, including coefficient (b) and standardized regression coefficient (β) for each significant predictor. In the coastal model, winter Secchi depth and SST were the most important predictors of Chl a , while in the open North Sea model, no significant predictor of Chl a was identifiable unless nutrients were excluded from the model (because of their short time series). A diagnostic Kolmogorov–Smirnov test was performed to ensure normality of the residuals: both models conformed to the assumptions of linear regression.

	Significant predictor	b	p	β	Model r^2	Model p	Model n	Model diagnostic
Coastal Chl a	Winter Secchi	0.085	0.017	0.564	0.510	0.015	15	0.682
	SST	0.318	0.045	0.455				
	Constant	0.173						
Open Chl a (nutrients excluded)	Atlantic inflow	0.883	0.014	0.364	0.112	0.014	45	0.392
	Constant	1.382						

-0.65 , $p = 0.001$) and TP ($r = -0.45$, $p = 0.029$) in coastal waters but an insignificant relationship with molar N:P ($r = 0.27$, $p = 0.216$). In addition to nutrients in coastal waters, coastal Chl a is negatively correlated with riverine nutrients as well (Elbe TN: $r = -0.69$, $p < 0.001$; Elbe TP: $r = -0.84$, $p < 0.001$; Rhine TN: $r = -0.36$, $p < 0.21$; and Rhine TP: $r = -0.77$, $p < 0.001$). Notice that the correlation between coastal Chl a and Rhine TN is not statistically significant; again this may be due to the short time series of Rhine TN.

Separate multiple linear regression analyses were performed on the coastal and open Chl a data sets (Table 2). In the coastal North Sea model, winter Secchi depth (standardized regression coefficient, β , = 0.564, $p = 0.017$) and SST ($\beta = 0.455$, $p = 0.045$) were the most important predictors of Chl a ($r^2 = 0.51$, $p = 0.015$, $n = 15$), while in the open North Sea model, no significant predictor was identified. Although no variable was significant when performing the multiple linear regression on the open North Sea, the exclusion of nutrients (because of their short time series, $n = 12$) showed that Atlantic inflow ($\beta = 0.364$, $p = 0.14$) is the best predictor of Chl a in the open North Sea, although the relationship is relatively weak ($r^2 = 0.112$, $p = 0.014$, $n = 45$). Neither model, therefore, featured nutrients (TN, TP, or N:P) as significant predictors of Chl a .

In summary, Chl a across the entire North Sea has displayed a rapid increase from the mid-1980s, culminating in the regime shift peak in 1989. After 1989, Chl a concentrations remained higher than in the pre-regime shift period in both the open and the coastal North Sea. Our results indicate that coastal Chl a is negatively correlated with coastal nutrient concentrations but positively correlated with winter Secchi depth and SST. Open North Sea Chl a shows no significant relationship with nutrients and is most closely correlated with Atlantic inflow, wind stress, and SST.

Discussion

It is well documented that in 1989 the North Sea experienced a strong peak in phytoplankton abundance (Reid et al. 1998) that has been correlated with warmer-than-average SST, a positive phase in the NAO, and increased oceanic inflow from the North Atlantic (Beaugrand 2004). This same peak, preceded by a rapid increase

in Chl a , can be clearly observed in the new coastal and open North Sea Chl a time series (Fig. 6). The rapid increase in Chl a beginning during the mid-1980s and peaking in 1989 is part of what is now thought to be a regime shift, a stepwise modification in the composition and productivity of an entire ecosystem at a regional scale, reflecting substantial hydrographic change (Reid and Edwards 2001; Reid et al. 2001a; Beaugrand 2004). At that point, the system converted to an alternate resilient state. As this sequence of events is nonlinear, a reduction of pressures on the system does not necessarily mean that the system will recover to a previous alternate state (Scheffer et al. 2001), a clear example of hysteresis.

Because riverine input is the primary vector through which anthropogenic nutrients enter the North Sea, nutrient concentrations in coastal North Sea waters are fundamentally linked to riverine nutrient concentrations and discharge (van Bennekom and Wetsteijn 1990; de Vries et al. 1998). Nutrient concentration data from the Elbe and Rhine rivers, important sources of nutrients to coastal waters, demonstrated a significant decrease in TN and TP since the early 1980s, while quantity of water discharged changed little (Figs. 4b,d, 5). This suggests that the decreased anthropogenic nutrient loads to the North Sea have occurred not because of decreased river discharge but more likely because of declining riverine nutrient levels. This is further supported by the positive correlations between riverine nutrients and coastal nutrient concentrations and negative relationship between riverine nutrients and coastal Chl a as well as the lack of relationships between coastal Chl a and Elbe and Rhine discharge (Table 1). Surprisingly, Elbe and Rhine discharge do not appear to be related to precipitation. This could be because the precipitation data used in this study are for the North Sea itself and not the river catchments. However, Elbe discharge is significantly negatively related to SST ($r = -0.32$, $p = 0.02$), although Rhine discharge is not ($r = -0.18$, $p = 0.19$).

The declining riverine nutrient load is reflected in the decreasing nutrient concentrations observed in coastal waters and has caused the current regime in the North Sea to be lower in coastal nutrient concentrations than the previous regime. Decadal means of TP and TN in coastal waters were nearly 50% higher in the 1980s (TN = 110.48 $\mu\text{mol L}^{-1}$, TP = 3.43 $\mu\text{mol L}^{-1}$) compared to the post-regime shift 1990s (TN = 56.03 $\mu\text{mol L}^{-1}$, TP = 1.97 $\mu\text{mol L}^{-1}$). Other studies have also observed declining

concentrations of phosphorus (de Vries et al. 1998; OSPAR Commission 2000; Nixon et al. 2003) and, to a lesser extent, nitrogen (de Vries et al. 1998; Nixon et al. 2003) in areas of the coastal North Sea in recent years. Agriculture is currently the main anthropogenic contributor of both N (63%) and P (45%) to North Sea waters (Nixon et al. 2003; Anonymous 2005). Since 1985, pollution from agricultural nitrates has been reduced by 21% (Nixon et al. 2003); part of this reduction can be attributed to the Nitrates Directive, which was adopted by the European Union in 1991 (European Union 1991a). Since 1985, agricultural P has been reduced by just 5% (Nixon et al. 2003). In 1991, the European Union also implemented the Urban Waste Water Treatment Directive (European Union 1991b). This directive has been partially responsible for the 42% decrease of N and the 78% decrease of P from urban wastewater treatment works since 1980 (Nixon et al. 2003). Since 1985, there have also been significant reductions in N and P loads from industry (81% P reduction, 79% N reduction) and other sectors (62% P reduction, 43% N reduction) (Nixon et al. 2003).

As concentrations of TN and TP have decreased, the molar ratio between N and P has steadily increased to >40:1 in coastal (Fig. 4c) and to >30:1 in riverine (Fig. 4d) waters; the change in N:P is potentially an artifact of the similar rate of decline in the two contrasting scales of concentrations. Since 1983, N:P has remained above the Redfield ratio of 16:1 in the coastal North Sea, while in the open North Sea, the ratio has stayed consistently below Redfield. Throughout our time series, both Elbe and Rhine waters have had an N:P greater than Redfield. Unlike the coastal North Sea, an increase in the N:P ratio is probably not observable for the open North Sea, as a trend in nutrient concentrations cannot be found because of insufficient data (Fig. 4a). However, as nutrient concentrations in the open North Sea are influenced predominantly by natural variability and not anthropogenic (riverine) sources (Lenhart et al. 1997), we would not expect to see as rapid a change in nutrient concentrations for open waters as we see for coastal and riverine waters. Therefore, as open North Sea nutrient concentrations change little, so does the N:P ratio. This suggests that P is presently the limiting nutrient in coastal North Sea waters while the open North Sea is N limited (Pätsch and Radach 1997). Studies in the Marsdiep (Philippart et al. 2000) and Helgoland (Radach et al. 1990; Hickel et al. 1992) have shown that a strong relationship exists between N:P and phytoplankton community composition, while laboratory experiments have demonstrated that a high N:P creates favorable conditions for *Phaeocystis*, a harmful algal bloom causing species (Riegman 1991; Riegman et al. 1992). Thus, further investigation is needed to determine the effects of change in the N:P on the wider coastal phytoplankton community composition.

As a consequence of the regime shift, biological changes to new alternate states are revealed in the new Chl *a* data sets. The data sets are in good agreement with changes observed previously for the PCI (Reid et al. 2001a) and then later confirmed and quantified on the basis of the PCI/SeaWiFS relationship for the North Atlantic and North

Sea as a whole (Raitsos et al. 2005). As mentioned previously, the regime shift is evident as a rapid increase followed by a consistently high level of Chl *a* in both coastal and open North Sea waters, but these changes cannot be explained by nutrients alone, as nutrient concentrations in the open North Sea have not changed significantly (Fig. 4a). The multiple linear regression models confirm this, as they too indicate that nutrients are not the best predictors of Chl *a* in either region of the North Sea (Table 2). After the regime shift, neither coastal nor open North Sea Chl *a* returned to its pre-regime shift level, but instead the time series indicates that the current North Sea regime maintains an average Chl *a* level 21% higher in the coastal zone and 13% higher in the open zone than that of the pre-1980 regime. Additionally, Chl *a* in coastal waters appears to be increasing still further, particularly in the southern North Sea (Fig. 6). Post-regime shift alterations to the North Sea ecology have also been observed, such as a change in the proportion of warm- and cold-water species of *Calanus* (Reid et al. 2003), trophic mismatch due to changes in phenology (Edwards and Richardson 2004), changes in distribution of horse mackerel (Reid et al. 2001a), and a collapse of cod stocks (Beaugrand et al. 2003). The current North Sea regime has fewer piscivorous top predators (Reid and Edwards 2001; Heath 2005) and a lower mean trophic level of fisheries landings (Pauly et al. 1998).

Although nutrient concentrations in the coastal North Sea have decreased significantly since the regime shift, algal biomass has continued to increase. The coincident decrease in nutrients and increase in Chl *a* is surprising, as, traditionally, increases in plankton production are triggered by increasing nutrients and are a symptom of eutrophication (Nixon 1995; Cloern 2001). In fact, areas of the coastal North Sea are commonly considered to be eutrophic (Hickel et al. 1993; Philippart et al. 2000; van Beusekom and de Jonge 2002), and eutrophication was identified as a key issue affecting the North Sea in the 1987 North Sea Quality Status Report (Reid and Edwards 2001).

While there is a strong relationship between algae and nutrients, it is considered to be nonlinear in coastal North Sea waters (i.e., a reduction in nutrient load does not lead to an equivalent reduction of phytoplankton biomass) (Lenhart 2001). Furthermore, as North Sea nutrient concentrations have decreased, water transparency has improved (Fig. 3), allowing the light-limited coastal phytoplankton (Pätsch and Radach 1997) to make better use of available nutrients. A similar increase in phytoplankton biomass was also documented in the Scheldt estuary, where the construction of a storm surge barrier caused reduced river flow with a corresponding increase in water transparency and decrease in nutrient concentrations (Westetyn and Kromkamp 1994). Improvement in water transparency has also been observed in the Western Wadden Sea (de Jonge et al. 1996) and Marsdiep (Bot and Colijn 1996). Although the explanation behind the increase in North Sea water transparency is still unclear, it may be linked to the increased inflow of warm, clear, oceanic water entering the North Sea (Reid et al. 2003). Additionally, multiple linear regression showed that Atlantic inflow is the best predictor

of Chl *a* in the open North Sea when nutrient data are excluded from the analysis. The transparency minimum (Fig. 3) occurring during the mid- to late 1970s is coincident with a period of reduced Atlantic inflow (Corten 1999) and low Chl *a* values in both the open and the coastal North Sea data sets (Fig. 6). This is in agreement with work by Edwards et al. (2001), who also attributed low PCI values in the late 1970s and early 1980s to a period of reduced Atlantic inflow. Additionally, the increasing water transparency that occurred throughout the 1980s and 1990s coincides with a proposed increase in Atlantic inflow during that period (Corten 1999; Edwards et al. 2001, 2002). The increase of indicator species with a southerly origin in the mid-1980s and sustained abundance thereafter in the North Sea (Corten 1999; Edwards et al. 2001) may indicate a change in current patterns, thereby increasing the volume of warm, clear, southerly water entering the North Sea from the North Atlantic (Edwards et al. 2001; Reid et al. 2001b).

However, the reduction in turbidity alone does not seem to be enough to explain the increase in Chl *a*, coincident with the decrease in nutrients. One possible explanation may be that after the regime shift, coastal waters have become more vulnerable to fluxes in nutrient concentrations. Because coastal phytoplankton are light limited, the cooler, more turbid state of the previous regime may have acted as a buffer, preventing algae from reaching the high biomass that is now possible. Multiple linear regression analysis supports this, indicating that while winter Secchi depth is the best single predictor of coastal Chl *a*, it explains only 30% ($p = 0.035$, $n = 15$) of the variability. Together, SST and winter Secchi depth form the best model, explaining 51% of the variation in coastal Chl *a* (Table 2). As mentioned previously, significant correlations exist between both open and coastal Chl *a* and mean annual SST. This result is in agreement with the previously established positive relationship between PCI and SST (Beaugrand and Reid 2003). The low Chl *a* values occurring in the late 1970s (Fig. 6) and the exceptionally high Chl *a* values observed in the late 1980s correspond to two hydroclimatic anomalies: the previously mentioned cold-boreal event in the late 1970s, associated with lower-than-average SST, and a warm-temperate event in the late 1990s associated with warmer-than-average SST (Edwards et al. 2002). Phytoplankton are closely linked to the temperature of their environment and respond to increased SST directly (physiologically), indirectly (enhanced or earlier stratification of the water column results in changes in phytoplankton succession), and phenologically (certain species are now experiencing earlier spring blooms) (Edwards and Richardson 2004; Richardson and Schoeman 2004). Additionally, warmer SST in the North Sea has created a longer growing season, thereby resulting in increased phytoplankton biomass, particularly during summer (Reid et al. 1998, 2001b) and winter (Reid et al. 2001b; Raitos et al. 2005). The enhanced response by the algal community to changes in nutrients is a characteristic of the new alternate state of the North Sea and may have triggered the other documented changes to the pelagic system. If, because of increased SST and clearer water,

coastal waters are indeed more sensitive to changes in nutrients, it is more important than ever that the quantity of anthropogenic nutrients entering the North Sea is reduced.

Alternatively, or additionally, to bottom-up (resource-limited) control, it is also important to consider the top-down (consumer-regulated) control of phytoplankton biomass. Fishing is an important industry in the North Sea, and the past few decades have seen changes in the catch of the top predators such as cod, haddock, and mackerel (Reid and Edwards 2001; Heath 2005). The decrease in piscivorous predators and the subsequent dominance of planktivorous fishes (sprat, sandeel, herring, and Norway pout) in the North Sea indicate that we are fishing down the food web (Pauly et al. 1998; Heath 2005). In theory, the resulting trophic cascade may have increased the consumption of zooplankton (Heath 2005) and therefore may also affect a subsequent lessening of grazing pressure on phytoplankton leading to an increase in algal biomass (Reid et al. 2000). However, data suggest that the top-down control of North Sea phytoplankton is important only during times of ecosystem stress (Riegman 1995; Reid et al. 2000). Additionally, Richardson and Schoeman (2004) suggest that bottom-up control dominates the North Sea plankton community. More research is needed to further quantify the importance of top-down control on North Sea phytoplankton biomass.

Therefore, it is suggested that changes in large-scale climatological forcing (possibly exacerbated by anthropogenic pressures such as overfishing) have gradually eroded the resilience of the North Sea system until a critical threshold was reached in the mid-1980s. Since then, the North Sea has been in an alternate state with its own characteristic ecological and environmental features. The present regime, though lower in nutrient concentrations, maintains a higher (and possibly still increasing) Chl *a* level in both coastal and open North Sea waters; this level of phytoplankton biomass in North Sea waters is more closely related to climatic variability via sea surface temperature and water transparency than nutrient concentrations.

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