

Regional climate change and harmful algal blooms in the northeast Atlantic

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Abstract

We investigated long-term spatial variability in a number of Harmful Algal Blooms (HABs) in the northeast Atlantic and North Sea using data from the Continuous Plankton Recorder. Over the last four decades, some dinoflagellate taxa showed pronounced variation in the south and east of the North Sea, with the most significant increases being restricted to the adjacent waters off Norway. There was also a general decrease along the eastern coast of the United Kingdom. The most prominent feature in the interannual bloom frequencies over the last four decades was the anomalously high values recorded in the late 1980s in the northern and central North Sea areas. The only mesoscale area in the northeast Atlantic to show a significant increase in bloom formation over the last decade was the Norwegian coastal region. The changing spatial patterns of HAB taxa and the frequency of bloom formation are discussed in relation to regional climate change, in particular, changes in temperature, salinity, and the North Atlantic Oscillation (NAO). Areas highly vulnerable to the effects of regional climate change on HABs are Norwegian coastal waters and the Skagerrak. Other vulnerable areas include Danish coastal waters, and to a lesser extent, the German and Dutch Bight and the northern Irish Sea. Quite apart from eutrophication, our results give a preview of what might happen to certain HAB genera under changing climatic conditions in temperate environments and their responses to variability of climate oscillations such as the NAO.

Globally, eutrophication is considered a major threat to the functioning of nearshore ecosystems, as it has been associated with the occurrence and a perceived increase of harmful algal blooms (HABs) (Anderson et al. 2002). HABs can have important ecological and economic consequences via their effects on coastal marine resources as well as other marine life and can endanger human health through shellfish poisoning and respiratory illness (Nixon 1995). Some authors have suggested that HABs are increasing globally due to anthropogenic influences (Smayda 1990; Hallegraeff 1993), including the North Sea (Richardson 1989), while

others have stressed that climate variability (apart from increased monitoring and awareness) are equally important (Sellner et al. 2003). The causes of the apparent increase in HABs is therefore yet unresolved. While there is certainly strong evidence that increased phytoplankton biomass and algal blooms are associated with elevated nutrients in some regions of the world (*see* review by Sellner et al. 2003), changes in the North Sea ecosystem are more problematic. For example, while elevated anthropogenic effects in the North Sea have been reported, there has been a contemporaneous period of marked climate change over the last few decades. Distinguishing the effects of anthropogenic eutrophication embedded within a climate signal is therefore extremely difficult and needs baseline data with extensive spatial and long temporal coverage. Any interpretation of the biological consequences of eutrophication is further exacerbated because many phytoplankton responses thought to be associated with increases in nutrients or changes in nutrient ratios can have equally plausible natural explanations. As a consequence, links between nutrient enrichment and environmental responses are difficult to discern and causative theories that link the two are unsubstantiated or unclear. While there have been many studies focusing on the role of

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eutrophication and HABs, there has been limited work on the role of climate oscillations (Rhodes et al. 1993; Belgrano et al. 1999) and very few on climate-change impacts. The main purpose of this study was therefore to investigate spatiotemporal patterns in HABs in relation to the major environmental changes that have occurred in the northeast Atlantic over the last few decades.

Arising from growing concerns of the apparent increase in the occurrence of HABs, a number of international and national initiatives have recently been implemented to improve and develop management and amelioration strategies. However, many of these initiatives unfortunately lack long-term and spatially extensive records. One of the few long-term datasets and the only one with extensive spatial records in the northeast Atlantic is the Continuous Plankton Recorder (CPR) survey. In the current study, we use CPR data in the northeast Atlantic to address whether (1) there is evidence of decadal spatial variability of HABs in the northeast Atlantic, i.e., whether there are any clear signs of HAB hot-spots in the northeast Atlantic, and (2) the frequency of bloom formation is increasing in the North Sea.

Materials and methods

Phytoplankton sampling by the CPR survey—The CPR survey is a long-term subsurface marine plankton monitoring program consisting of a network of transects towed monthly across the major geographical regions of the North Atlantic. On some standard routes, there exists a virtually unbroken monthly coverage back to 1946. After each tow, CPR samples are returned to the laboratory for routine analysis, including the estimation of phytoplankton biomass (phytoplankton color index) and the identification of up to 500 different phytoplankton and zooplankton taxa (Warner and Hays 1994). Phytoplankton analysis is split into two stages. First, the phytoplankton color index is assessed on an ordinal scale, by reference to standard color charts, to obtain an estimate of the quantity and density of phytoplankton recorded by the visual discoloration on the CPR silk produced by green chlorophyll pigments (phytoplankton biomass estimate). The latter includes the chloroplasts of broken cells and small unarmored flagellates, which tend to disintegrate when they contact formaldehyde (Reid et al. 1987). For mathematical purposes, the four rank-order categories of phytoplankton color have been assigned numerical values on a ratio scale (Colebrook and Robinson 1965). Direct comparisons between the phytoplankton color index and other chlorophyll *a* estimates, including SeaWiFS satellite estimates, indicate strong positive correlations (Batten et al. 2003a). The second stage of phytoplankton analysis involves counting phytoplankton cells under high magnification ($\times 450$), representing a subsample covering 0.0001% of the sample. Each CPR sample represents $\sim 3 \text{ m}^3$ of filtered seawater. Using this analysis method, 170 phytoplankton taxa have been routinely identified and counted by the CPR survey since 1958. For the purpose of this study, we specifically focused on dinoflagellates. While HABs do also include some diatom species (e.g., *Pseudo-Nitzschia* spp.), the apparent global increase in HABs normally refers to the in-

crease in noxious and toxic flagellate species (Smayda and Reynolds 2001).

Geostatistical methodology and data analysis—Due to the irregular spacing of CPR sampling, geostatistical gridded estimates were used to examine spatial and temporal variability of dinoflagellate abundance in the northeast Atlantic ($47^\circ\text{--}60^\circ\text{N}$; $15^\circ\text{W--}10^\circ\text{E}$). Using 83,240 CPR samples, data were first temporally partitioned into monthly datasets, resulting in 552 spatially interpolated gridded datasets per taxa, before calculating mean spatial distributions over time. In this study, we have used mean decadal spatial distributions (1960s, 1970s, 1980s, and post-1990s) to represent spatiotemporal variability. Nodal estimates were calculated using the inverse-distance method (Isaaks and Srivastava 1989) at a grid resolution of 0.5° latitude by 0.5° longitude with an omnidirectional quadrant search of 250-km radius. Cell counts were log transformed $\log(x + 1)$. For the geostatistical analysis of CPR data, four common and well-sampled bloom-forming dinoflagellates were used: *Prorocentrum* spp., *Ceratium furca*, *Dinophysis* spp., and *Noctiluca scintillans*. *Prorocentrum* spp. (in particular *Prorocentrum lima*) and *Dinophysis* spp. are both associated with toxic-forming blooms (diarrhetic shellfish poisoning), whereas *C. furca*, *Prorocentrum* spp. (in particular *P. micans*, the dominant species recorded by the CPR survey) and *N. scintillans* are associated with detrimental effects on the marine ecosystem via anoxic events.

The dinoflagellate and diatom time series were calculated using the total cell counts of all species/taxa numerically counted. Cumulative sums and standardized anomaly plots were applied to summarize major changes and identify phase transitions in the phytoplankton time series. The cumulative function results in the smoothing of high frequency (inter-annual) variability and highlights changes in the local mean values along the time series (Beaugrand et al. 2000). Successive negative residuals below the mean will result in a negative slope and successive positive residuals above the mean will result in a positive slope. Generally, the cumulative sum will only show the major shift (i.e., one major signal) in the time series.

To represent interannual variability in dinoflagellate blooms, we used both an assessment of the frequency of exceptional blooms and encapsulated the interannual changes in abundances of the dinoflagellate taxa using principal component analysis. As the precise definition of a bloom is problematic, we used two indices to represent interannual changes in HAB formation, as an increase in dinoflagellate abundance does not necessarily equate to an increase in the number of blooms and vice versa. To define an exceptional bloom using CPR data, we used the value of 2 SD above the species long-term monthly mean (1958–2002). To calculate interannual changes in the number of blooms in various regions (CPR standard areas) in the North Sea, we summed the number of species occurring above 2 SD in relation to the number of CPR samples in a given region representing an annual percentage of bloom frequencies. The sum of annual bloom frequencies represented major blooms of the genera *Ceratium*, *Dinophysis*, *Protoperdinium*, and *Prorocentrum*. The second measure of HAB formation was

based on standardized principal component analysis of the abundance of all dinoflagellate taxa that occurred on more than 1% frequency of samples from 1958 to 2002. This included six species of the *Ceratium* genus, *Dinophysis* spp., *Prorocentrum* spp., and *Protoperidinium* spp. *N. scintillans* was not used in either index because it has only been numerically counted since 1981. Principal component analysis (PCA) is a standard statistical procedure for reducing multivariate data that has been used extensively at the CPR survey for summarizing multiple time series (see Colebrook 1978; Beaugrand et al. 2003; Beaugrand 2004 for more details on the method). Here, the first PCA represents the dominant mode of variability in multivariate time series.

In area B1, where there has been the largest increase in HABs, we investigated the potential underlying environmental causes. One of the difficulties was obtaining datasets over the required time and space scales for this study. Unfortunately, there were insufficient nutrient data in the area over the last 45 years to identify interannual changes in surface concentrations, so we used two indirect measures of nutrient enrichment: viz., wind mixing and Atlantic inflow into the North Sea (updated from Iversen et al. 2002). Wind speed was obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) database for our area of interest between April and September on a 2° resolution. In terms of broader scale enrichment, 90% of the nutrients entering the North Sea are from Atlantic water entering from the north (NSTF 1993). As there are no time series of measured inflow over the time scale of the present study, we have used the flux of Atlantic waters entering the North Sea between the Orkney Islands and Utsira from the NORWECOM three-dimensional hydrodynamic model. Inflow is greatest from January to March (Iversen et al. 2002), and we have calculated inflow each year over this period. We have also used two indices of stratification: viz., surface temperature and salinity. We calculated mean annual sea surface temperature (SST) from the Hadley Center, UK Met Office (HadISST Version 1.1). Surface salinity data were obtained from the International Council for the Exploration of the Sea (ICES) database (see <http://www.ices.dk/ocean/>). To summarize the simultaneous interannual changes in these four environmental variables, we have performed a standardized PCA. To assess the relationship between interannual changes in dinoflagellate taxa and environmental variables, we used Pearson correlation. Because our physical and biological time series are serially autocorrelated, we have adjusted our correlation procedure by reducing the effective number of degrees of freedom according to the modified Chelton method (Pyper and Peterman 1998).

Potential biases and limitations—Due to the mesh size of CPR silks, many phytoplankton species are only semiquantitatively sampled due to the small size of the organisms. There is thus a bias toward recording larger armored flagellates and chain-forming diatoms, and smaller species abundance estimates from cell counts will probably be underestimated in relation to other sampling methods. However, Robinson (1970) found that the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution, and composition (i.e., the per-

centage retention is roughly constant within each species even for very small-celled species, such as *Asterionellopsis glacialis* and *Skeletonema costatum*). To obtain robust time series and spatial maps, only the most commonly recorded dinoflagellate taxa were examined in this study. Therefore, generalizations based on this study concerning long-term changes in HAB taxa as a collective entity must be treated with some caution. A thorough statistical analysis of HAB trends in relation to nutrients could not be attempted in this study due to spatial and temporal limitations in availability of data and at the scale of the CPR survey. Due to the subsurface sampling (~7 m) of the CPR, the survey cannot take into account long-term changes in the depth of the pycnocline. If there were significant changes to the depth of the pycnocline over a decadal time scale, this could potentially bias CPR results. Due to the lack of sufficient physical data at the same scales of this study, this potential bias could not be tested. It is worth noting, however, that the water immediately behind a large, fast-moving vessel is likely to be mixed and homogenized well below the CPR towing depth (Batten et al. 2003b). For further details on the technical background, methods, consistency, and comparability of CPR sampling, see Batten et al. (2003b).

It is estimated that ~90% of the inputs to the North Sea of both the major nutrients nitrate and phosphate, needed for phytoplankton growth, derive from the North Atlantic (NSTF 1993). Anthropogenic inputs of nutrients and eutrophication effects are therefore believed to primarily affect the coastal zone, in particular, estuaries and fjords with limited water exchange, such as the Wadden Sea, the German Bight, the Kattegat, and the eastern Skagerrak. CPR sampling in most cases samples areas further than 1 km offshore and may miss the effects of eutrophication in areas very close to the shore. In most cases, patterns and trends found using CPR data are therefore more likely to be associated with large-scale hydroclimatic rather than local anthropogenic signals.

Results

Long-term trends in phytoplankton functional groups—To explore temporal and spatial fluctuations in marine dinoflagellate HABs, it was first necessary to examine some of the macroscale patterns of the phytoplankton functional groups. The standardized anomaly plots, Fig. 1, show the long-term monthly variability of phytoplankton biomass (1948–2002), dinoflagellate cell counts (1958–2002), diatom cell counts (1958–2002), and SST (1948–2002) in the central North Sea. These plots highlight the major changes in the North Sea environment in the late 1980s and in particular show that the North Sea has remained in a warm state since the end of the 1980s. The major change in temperature is reflected in phytoplankton biomass and dinoflagellate abundance, which showed similar changes around this period. While total diatom abundance has been in decline since the 1960s, the winter assemblages of diatoms have clearly increased in abundance during the 1990s (Fig. 1d). The cumulative sum analysis shown in Fig. 2 emphasizes the change in total phytoplankton biomass, SST, and the winter cell counts of di-

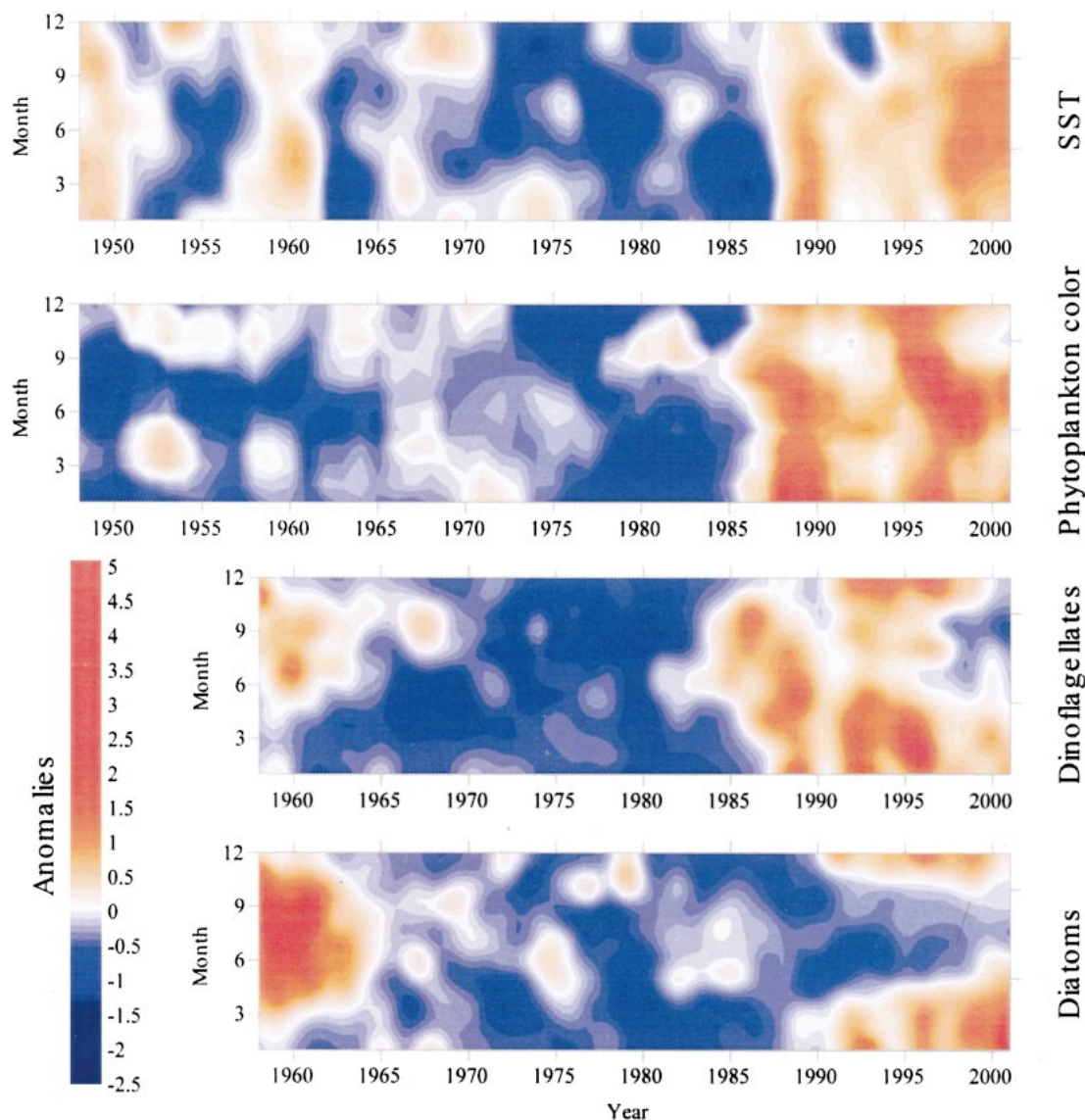


Fig. 1. Monthly standardized anomaly plots for (a) sea surface temperature (1948–2002), (b) phytoplankton color (1948–2002), (c) dinoflagellate cell counts (1958–2002), (d) diatom cell counts (1958–2002). Shades of red signify values above the long-term mean and shades of blue values below the long-term mean. Zero-mean values are in white. Data averaged for the central North Sea.

noflagellates and diatoms during the late 1980s in the North Sea. The environmental change or phase transition in the late 1980s is not only restricted to the functional groups of phytoplankton but has influenced zooplankton and both the benthos and fisheries (Reid and Edwards 2001; Beaugrand and Reid 2003). The structural reorganization of marine ecosystems that occurred during this period has been termed a regime shift and has been associated with changes in the North Atlantic Oscillation, increased oceanic inflow into the North Sea, and trends in the Northern Hemisphere temperature regime (Beaugrand 2004). A pronounced decrease in sub-Arctic zooplankton and an increase in warm-temperate species also occurred during this period, suggesting a shift in the North Sea to a warm-temperate ecosystem (Beaugrand et al. 2002). It is likely that biogeographical boundary shifts in phytoplankton assemblages, not yet studied in any detail,

have also occurred during the 1990s, resulting in further changes in species composition. Recent work by Edwards and Richardson (2004) has also shown that climate warming has influenced the phenology of plankton, with the earlier seasonal appearance of dinoflagellates significantly correlated with SST.

Decadal spatiotemporal variability in HABs—Significant changes in spatial distributions have occurred over the last four decades for the four key dinoflagellate taxa examined (Fig. 3). The distribution of *Prorocentrum* spp. was most abundant in oceanic waters to the southwest of the British Isles and the Celtic Sea during the 1960s. During the 1970s and 1980s, the genus was most prevalent along the Celtic and western English Channel frontal boundaries, and also in the North Sea in the Firth of Forth. Since the 1960s, the

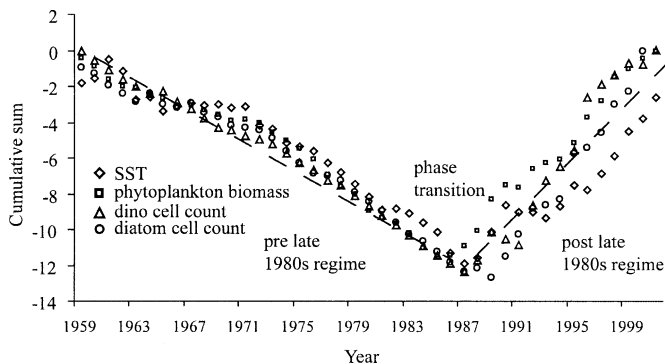


Fig. 2. Cumulative sum analysis of standardized data, highlighting phase transitions, and biological shifts. Successive negative residuals below the mean indicate a negative slope, successive positive residuals above the mean indicate a positive slope. This procedure results in the smoothing of small interannual fluctuations and highlights changes in the local mean values along the time series. Data averaged for the central North Sea.

genus has become progressively more abundant in the North Sea, being mainly restricted to a small area of the German Bight in the 1960s to abundant throughout the North Sea during the 1990s. The spatial distribution of the ubiquitous *C. furca* (a numerically dominant dinoflagellate in the northeast Atlantic) has remained fairly similar over the last four decades, being most abundant in the central North Sea and oceanic waters west and northwest of Ireland. During the 1970s and 1980s, the species was abundant along the Flamborough Front in the central North Sea; since the post-1990s, however, the center of North Sea distribution has moved further north. The distribution of *Dinophysis* spp. over the last four decades has shown a movement of its center of distribution from the west of the North Sea to the east of the North Sea. During the 1970s, high abundances of *Dinophysis* spp. were geographically centered along the east coast of the United Kingdom, whereas highest abundances were found along the west coast of Denmark during the 1980s. Similar to *C. furca*, the center of distribution of *Dinophysis* spp. during the 1990s appears to have shifted slightly northward. As *N. scintillans* has only been counted numerically in CPR samples since 1981, only the 1980s and post-1990s spatial distributions are shown. The spatial distribution of *N. scintillans* has remained relatively unchanged throughout the two periods, but has increased in the post-1990s, particularly along the Dutch coast, the western English Channel, and in the northern Irish Sea. Examining the anomaly maps (the difference between the distributions in the post-1990s and the average distribution from the period 1960–1989), two dominant patterns were prominent in the northeast Atlantic. First, the increases in both *Prorocentrum* spp. and *N. scintillans* are most pronounced in the south and east of the North Sea. Second, both the increases in *Dinophysis* spp. and *C. furca* are restricted to the adjacent waters off Norway (following closely to the offshore limit of the summer surface 34 isohaline). The abundance of both taxa has diminished along the eastern coast of the United Kingdom and in the southern coastal North Sea.

Frequency of blooms—Using standard CPR regional areas, the percent frequency of exceptional blooms and annual means of the first PCA of dinoflagellates were examined from the period 1958–2002 (Fig. 4). The most consistent feature regionally in the interannual variability of bloom frequencies over the last four decades was the anomalously high values recorded in the late 1980s. This anomaly is present in the northern and central North Sea areas (standard areas B2 in 1987, B1 in 1988, and C2 and C1 in 1989). For example, while the percentage of exceptional blooms on CPR samples is ~5% per year, the exceptional bloom frequency was nearly 60% in area B1 during 1988. The decadal variability of exceptional bloom frequencies, however, showed no obvious signs of significant trends in most areas, apart from a small decline in the southern North Sea and an increase in the B1 area (west coast of Norway). There has clearly been an increase in the percentage of exceptional bloom frequencies over the last 10 years in this area (Fig. 4), with the last 6 years all above 10% exceptional bloom frequency and with the post-90s distribution of *Dinophysis* spp. and *C. furca* showing increased abundance in this area. Virtually all dinoflagellate abundances have increased in this region over the last 10 years, including other *Ceratium* species, *Dinophysis*, *Protoperdinium*, and *Prorocentrum* genera (all had positive loadings on dinoflagellate PC1). It must be noted, however, that a rise in exceptional bloom frequencies does not necessarily equate to a rise in annual abundance or vice versa, although there is fairly good fit between the two measures. While there is no evidence of increasing bloom formation in the central and southern North Sea during the last decade, it is clear from Fig. 3 that the abundances of certain taxa are increasing in these areas. In area B1, where there has been the largest increase in HABs, we investigated the potential underlying environmental causes (Fig. 5). A strong significant correlation was evident between the increase in dinoflagellate taxa (Dino PC1) and environmental variability (Env PC1); $r^2 = 0.487$, $p < 0.01$.

Discussion

The suggestion that HABs have been increasing globally in recent years is of considerable environmental concern (Smayda 1990). This study has shown that HABs are indeed increasing in some areas of the northeast Atlantic, although the increase is not spatially homogenous and is restricted to specific habitat types. While there have been many studies focusing on the role of eutrophication and HABs, there has been limited work on the role of climate oscillations (Rhodes et al. 1993; Belgrano et al. 1999) and very few on climate change impacts. At the regional to oceanic scale (and at the sampling scale of the CPR survey), climate variability and regional climate warming appear to play a dominant role in the long-term changes in phytoplankton assemblages and biomass (Reid et al. 1998; Edwards et al. 2002; Richardson and Schoeman 2004). Summarizing the long-term changes in functional groups of phytoplankton, the significant hydroclimatic changes that have occurred since the late 1980s and have continued to the present have resulted in an environment that favors the growth and earlier succession (Edwards

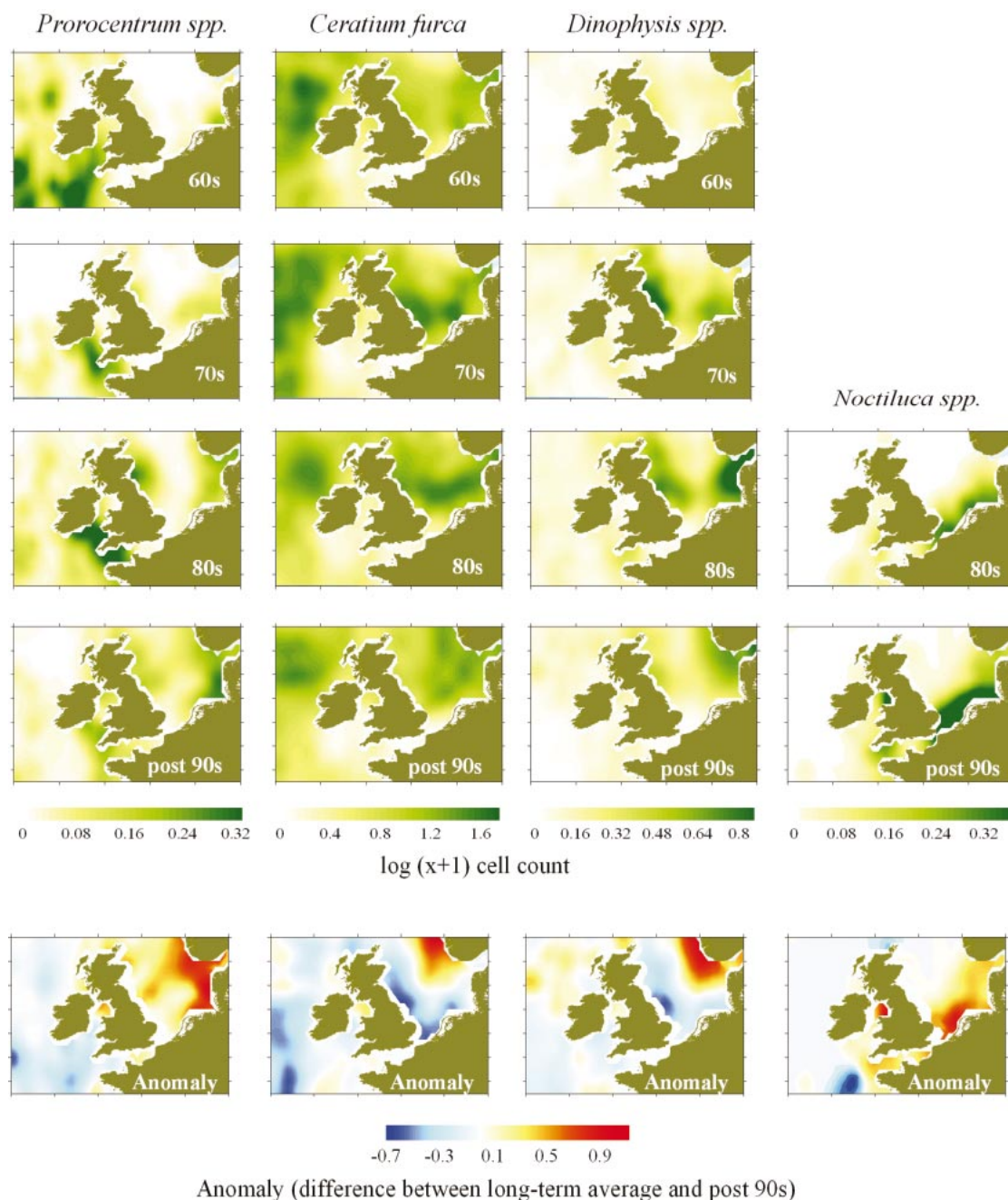


Fig. 3. Geostatistical estimates of the decadal mean spatial distribution of four dinoflagellate taxa in the northeast Atlantic. Estimated cell counts were $\log(x + 1)$ transformed. Anomaly maps signify the difference between the long-term mean (1960–1989) and post-1990s (1990–2002) distributions. Shades of red signify values above the long-term mean and shades of blue signify values below the long-term mean. Zero-mean values are in white.

and Richardson 2004) of flagellates and dinoflagellates in the North Sea. In the North Sea, dinoflagellates are positively correlated with the North Atlantic Oscillation (NAO) and SST, whereas diatoms are negatively correlated (Edwards et al. 2001). Other long-term phytoplankton studies in the North Sea have also noted similar ecological changes occurring around the late 1980s (Fock 2003) and, in particular, an increase in the ratio of dinoflagellates versus diatoms in the southern North Sea (Hickel 1998). Similar changes

were evident in the Baltic Sea: since 1988/1989, a general decline in diatoms has been observed and dinoflagellates have become more dominant (Wasmund et al. 1998). The dominance of dinoflagellates was related to milder winter temperatures. In the context of HABs, if these climatic changes persist, they may lead to the emergence of a new successional regime in phytoplankton (whether by adaptation or by a shift in species composition) and the earlier and more frequent formation of dinoflagellate blooms in some

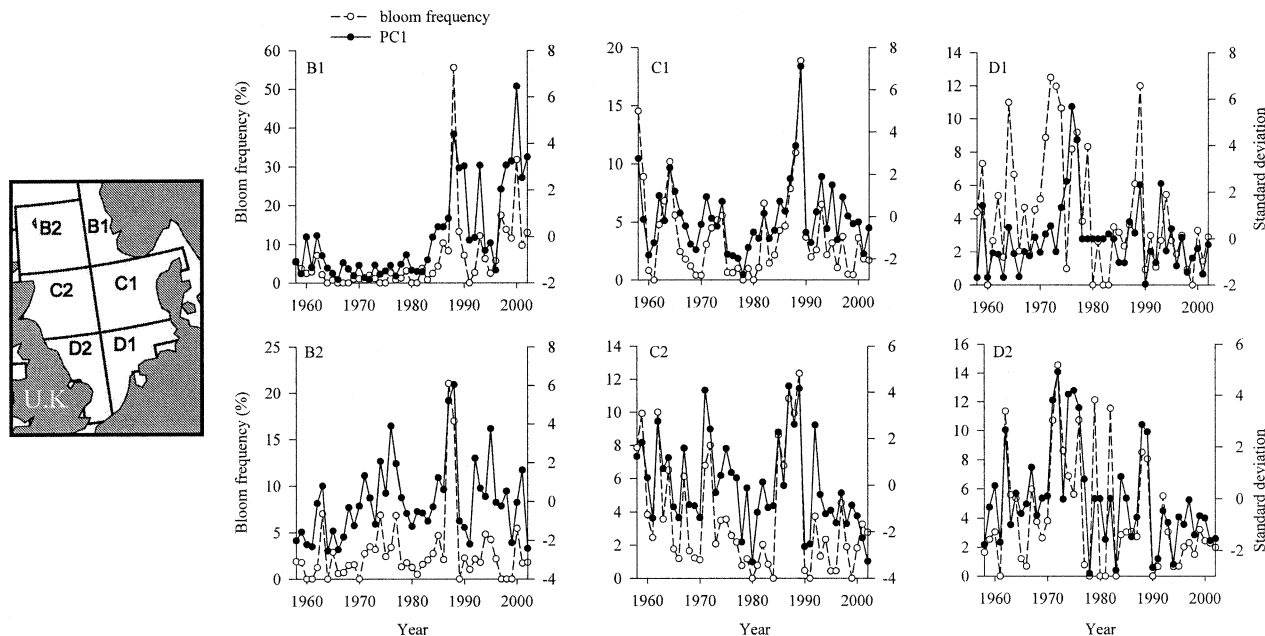


Fig. 4. Interannual changes in the number of blooms represented by bloom frequency and the first PCA of dinoflagellates (standard deviations) in various regions (standard CPR boxes) for the North Sea from 1958–2002. Interannual changes represent the number of species occurring above 2 SD in relation to the number of CPR samples in a given region representing an annual percentage of bloom frequencies. The collective sum of annual bloom frequencies represented variability in the *Ceratium*, *Dinophysis*, *Protoperdinium*, and *Prorocentrum* genera.

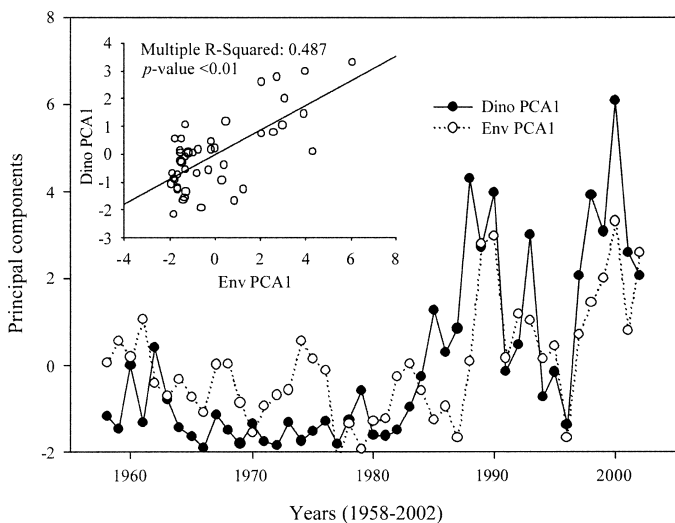


Fig. 5. Interannual changes in the abundance of the dinoflagellate taxa and environmental variability represented by the first PCA (PC1) for standard CPR area B1 from 1958 to 2002 and resultant regression. Dinoflagellate PC1 included dinoflagellate taxa that occurred more than 1% by frequency of samples from 1958 to 2002 (including six species of the *Ceratium* genus, *Dinophysis* spp., *Prorocentrum* spp., and *Protoperdinium* spp.). Environmental PC1 included Atlantic inflow, salinity, sea-surface temperature, and wind speed. Correlation was adjusted for temporal autocorrelation using the modified Chelton method (Pyper and Peterman 1998).

areas of the North Sea. Dinoflagellates may not only be responding physiologically to temperature, but may also respond to temperature indirectly if climate warming enhances stratified conditions or if these conditions appear earlier in the season (Edwards and Richardson 2004). The decrease in viscosity associated with increased temperature may also play a role in favoring dinoflagellate and flagellate dominance if warming is faster than diatom adaptations, but its true effect is still relatively unknown (Peperzak 2003).

In a more genus-specific context, the increase in the abundance of the genera *Ceratium*, *Dinophysis*, *Protoperdinium*, and *Prorocentrum* appear to be related to hydroclimatic changes that have manifested most conspicuously off the coast of Norway. In particular, recent large HAB blooms appear to be associated with warm temperatures coupled with the general decrease in salinity in the Norwegian Coastal Current (Sætre et al. 2003). The long-term decreasing trend in salinity is probably caused by the increase in precipitation and substantial increase in runoff associated with positive values of the NAO (Gjøsæter et al. 2000; Christensen et al. 2001; Sætre et al. 2003). These changes are also likely to have enhanced the nutrient export to marine waters from terrestrial sources, which may have further enhanced the formation of phytoplankton blooms in the Skagerrak and in Norwegian coastal waters (Gjøsæter et al. 2000). Using a shorter time series and at one sample location off the coast of Sweden, Belgrano et al. (1999) found a significant correlation between the abundance of *Dinophysis* spp. with the NAO index. In experimental studies, the physiological response to climate warming has been studied for a number of HAB taxa (Peperzak 2003). Climate-warming scenarios

(expressed as an increase of 4°C) coupled with water-column stratification led to a doubling of growth rates of potentially harmful dinoflagellates of *Dinophysis* spp. and *Prorocentrum* spp. (Peperzak 2003). According to our results, *Prorocentrum* spp. has increased most markedly over the last decade in the German Bight and in Danish coastal waters (Fig. 3). This is in accordance with geographical areas that show the warmest summer temperatures in the North Sea. A significant positive relationship between the long-term abundance of *Prorocentrum* spp. and SST was found in this region (Box D1, $r = 0.46$, $p < 0.001$).

With the progressive warming of the northeast Atlantic over the last few decades, *Prorocentrum* spp. seems to have shown evidence of a biogeographical shift in populations. The distribution of *Prorocentrum* spp. was most abundant in oceanic waters to the southwest of the British Isles and the Celtic Sea during the 1960s. Since then, the genus has become progressively more abundant in the North Sea, being mainly restricted to a small area of the German Bight in the 1960s to abundant levels throughout the North Sea during the 1990s (Fig. 3). Biogeographical boundary shifts mediated by climate change in phytoplankton populations also have the potential in the future to lead to the occurrence of species with southern biogeographical affinities not yet considered to be detrimental in certain areas of the North Sea. While the distribution of *N. scintillans* has remained relatively unchanged throughout the last two decades, it has considerably increased in abundance during the post-1990s, particularly along the Dutch coast, the western English Channel, and in the northern Irish Sea. Again, it is likely that warming temperatures have played a role in this pattern, with the increase in *N. scintillans* from the Helgoland Roads (a separate long-term plankton study) time series being linked to warmer winter SST and the NAO index (Heyen et al. 1998). Further, the seasonality of *N. scintillans* has shown a correlation with seasonal ambient temperatures (Greve 2004). We also found a strong significant positive correlation between the long-term abundance of *N. scintillans* and SST in this region (Box D1, $r = 0.61$, $p < 0.001$).

The most consistent feature regionally in the interannual variability of bloom abundances over the last four decades was the anomalously high values recorded in the late 1980s in the northern and central North Sea areas. Explaining detailed mechanisms behind this exceptional event is difficult, but it was driven by anomalous ocean climate conditions, including a large oceanic incursion into the North Sea (Edwards et al. 2002). The timing of the exceptional dinoflagellate blooms coincided with unprecedented blooms of the oceanic indicator diatom *Thalassiothrix longissima* in area B2 in the autumn of 1987 and spring of 1988 and area C2 and C1, including the Skagerrak, in the spring of 1989 (data not shown). Area B1, which encompasses the Norwegian Coastal Current, did not show any signs of a bloom of *T. longissima*, most likely due to the low salinities encountered in this area. This period was also associated with a substantial increase in the catch of horse mackerel (*Trachurus trachurus*) in the northern North Sea from 1987 to the present, again related to the increase in transport of Atlantic water (Iversen et al. 2002). At the regional scale, the ecological state of the North Sea is strongly influenced by the inflow

of oceanic water from the Atlantic Ocean, which enters from the north via the Orkney and Shetland Isles and along the Norwegian Trench and in the south through the English Channel. The vast majority of Atlantic water entering the North Sea traveling south along the Norwegian Trench will eventually leave the North Sea via the Skagerrak and travel northward along the Norwegian coast, taking between a few months and 1 year (Iversen et al. 2002). The large phytoplankton biomass and *Dinophysis* blooms recorded off the coast of Sweden during this period were also associated with inflowing Atlantic water related to positive NAO values (Belgrano et al. 1999). This period also coincided with one of the most globally known and widely reported bloom events to occur over the last few decades. The *Chrysochromulina* bloom off the Norwegian Skagerrak coast in 1988 not only caused widespread ecological disturbances but was estimated to have caused an economic loss for the fish-farming community of ~10 million Euro (Skjoldal and Dundas 1991). The bloom in this area was again associated with warm temperatures and low salinities, resulting in highly stable conditions encountered in the Norwegian Coastal Current and was associated with the NAO index (Gjøsæter et al. 2000).

Danielssen et al. (1997) earlier stressed that the temporal and spatial distribution of phytoplankton in the Skagerrak may be related to the variability in the inflow of nutrient-rich Atlantic water, as well as low-salinity Baltic water (Lindahl et al. 2003). As mentioned earlier, this period was also associated with a shift in the phytoplankton community from diatoms to dinoflagellates noted in the North Sea and in the Baltic. During the 1990s off the Swedish west coast, there has also been a decrease in deep-water oxygen concentrations, which is thought to be caused by higher net primary production and an increase in sedimentation during the 1990s (Lindahl et al. 2003). Although not classed as an HAB, coccolithophores also form large blooms in this area (data not shown). Recent research by Smyth et al. (2004) found a strong correlation between satellite-detected coccolithophore activity and warm-temperature and low-salinity events off the northern coast of Norway and the Barents Sea. It seems likely that an important environmental impact caused by climate change is an increase in the presence of haline stratification in regions susceptible to freshwater inputs resulting in an increase in bloom formation. For example, on the other side of the Atlantic, in the Grand Banks region, we have witnessed similar changes to the diatom/dinoflagellate ratio, with an increasing abundance of dinoflagellate species (notably *Ceratium arcticum*) (Johns et al. 2003). These changes, since the early 1990s, have been linked to hydroclimatic variations, specifically increased stratification and stability in the region and indicate a progressive freshening of this region likely caused by regional climate warming.

Although dinoflagellates have a variety of adaptive strategies and resultant habitat preferences (Smayda and Reynolds 2001), a number of community assemblages (*Ceratium*, *Dinophysis*, *Prorocentrum*, and *Prorocentrum* genera) found in this study are responding in similar ways, particularly with respect to low-salinity and warm-temperature events off the Norwegian coast. As a result, while the few

species of HABs studied in this article do not represent all the variation in the numerous phytoplankton species associated with the formation of HABs, they can serve as a proxy for certain genera of what might be broadly emerging under climate change conditions in temperate environments and in the variability of climate oscillations such as the NAO. In summary, climate change has direct physiological effects through enhanced growth and reproduction of some dinoflagellate species and indirectly by modifying the environment, both by increased temperature and, in some areas, precipitation, toward more stable stratified conditions. From these results, expected biological manifestations of climate change on dinoflagellates are likely to include an increase in blooms of certain taxa (e.g., *N. scintillans*, *Prorocentrum* spp.), leading to an increase in toxic and anoxic events in some areas, phenological changes, biogeographical shifts, and the appearance of species new to the North Sea. According to our results, areas in the northeast Atlantic highly vulnerable to the occurrence of these changes are the Norwegian Coastal Current area and the Skagerrak. According to geological records taken from Atlantic and Pacific Canada when summer SST was much warmer during the late glacial–early Holocene (up to 5°C), there was a period of sustained high production of red-tide blooms (Mudie et al. 2002). The high production of red-tide blooms was associated with the warmer SST and led the authors to suggest that global warming is strongly implicated in the historical increase in the frequency of red tides and other HABs (see also Dale 2001).

While direct mechanisms elude us for all regional areas in this current study, the increase in the occurrence of dinoflagellate HABs in Norwegian coastal waters is strongly associated with the unusual ocean hydroclimatic conditions prevailing in this region during the 1990s. Apart from the general warming of the North Sea since the late 1980s (associated with the increase in *N. scintillans* and to a lesser extent *Prorocentrum* spp.), these areas seem to be doubly susceptible to the oscillations of the NAO through advective processes by both being influenced by the NAO from increasing inflow from oceanic sources and outflow of low-salinity and perhaps nutrient-rich coastal water (Danielssen et al. 1997; Belgrano et al. 1999; Sætre et al. 2003). These changes have resulted in exceptionally anomalous exchange circulation in the Skagerrak during the 1990s (Schrum et al. 2004). These conditions may favor and enhance the formation of dinoflagellate blooms both by increasing nutrient availability and density stratification during the summer months in the Norwegian Coastal Current. Other vulnerable areas include Danish coastal waters and, to a lesser extent, the German and Dutch Bight (which also experiences significant freshwater input) and the northern Irish Sea. At the scale of this study, from the regional to the northeast Atlantic, it appears that climate oscillations and warming play an important role in governing fluctuations of some HABs from exceptional blooms to long-term decadal trends. Unfortunately, some of the regions noted above that are most susceptible to hydroclimatic fluctuations are also thought to be vulnerable to elevated nutrient concentrations. Phytoplankton structural changes and blooms attributed to climate change could therefore be reinforced or accentuated by anthropogenic nutrient input into these areas.

While research focused on establishing causal links between algal changes and eutrophication is needed to further our understanding of anthropogenic changes on our coastal seas, consideration also needs to be given to the wider scale natural environmental changes on algal populations. Without such studies, bloom events may be incorrectly attributed to eutrophication, while the real modifier of change could be climatic in origin. For example, many temporal studies in the North Sea have initially interpreted abrupt changes in the biology of the North Sea as signs of nutrient enrichment; however, when regional comparisons were taken into consideration, the biological patterns that emerged were found to be part of far-field North Atlantic hydroclimatic changes (Edwards et al. 2002). These findings stress the need not only for an ecological approach to monitoring human affects but for incorporating multiscale future monitoring strategies that quantify some degree of natural variability from the regional scale down to the local scale. It is only when these wider scale Atlantic influences and climatic oscillations have been taken into consideration that we can be confident in assessments of eutrophication impacts on the biology found in European waters.

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