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Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic

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Abstract

The Continuous Plankton Recorder (CPR) survey has been used to characterize phytoplankton and zooplankton space–time dynamics in the North Sea since 1931 and in the North Atlantic since 1939. Phytoplankton biomass is assessed from these samples by visual assessment of the green color of the silk mesh, the Phytoplankton Color Index (PCI), and the total count of diatoms and dinoflagellates. Species with a frequency of occurrence greater than 1% in the samples are used as indicator species of the community. We investigated (1) long-term fluctuations of phytoplankton biomass, total diatoms, and total dinoflagellates; (2) geographical variation of patterns; (3) the relationship between phytoplankton and climate forcing in the North Atlantic CPR samples; (4) the relative contribution of diatoms and dinoflagellates to the PCI; and (5) the fluctuations of the dominant species over the period of survey to provide more information on the processes linking climate to changes in the phytoplankton community. As a result of the differences in microscopic analysis methods prior to 1958, our analyses were conducted for the period ranging from 1958 to 2002. The North Atlantic was divided into six regions identified through bathymetric criteria and separated along a North–South axis. Based on 12 monthly time series, we demonstrate increasing trends in PCI and total dinoflagellates and a decrease in total diatoms.

Individuals and populations are intrinsically linked to the changes occurring in their environment at many spatial and temporal scales (Legendre and Demers 1984). Being at the base of the marine food-web, information on phytoplankton long-term trends is an absolute prerequisite to the understanding of biological responses to natural oscillations within this environment. In this framework, the Continuous Plankton Recorder (CPR) survey has been deployed since 1931 to describe and analyze plankton variability in the North Atlantic and North Sea and to interpret this variability in relation to fisheries and atmospheric climate events (Robinson and Hiby 1978). It is one of the few marine long-term biological monitoring programs and the only one providing a systematic coverage of the Northeast Atlantic and the North Sea in space and time.

The CPR survey measures the abundance and variability of up to 400 phytoplankton and zooplankton taxa and provides a visual assessment of phytoplankton biomass known as the Phytoplankton Color Index (PCI). The PCI is based on four color categories and has been shown to be a relevant index of in situ chlorophyll concentration (Batten et al. 2003). Furthermore, it has been extensively used to describe the seasonal and long-term patterns of phytoplankton abundance in various regions of the North Atlantic (Edwards et al. 2001).

Acknowledgments
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A recent study based on CPR samples showed that much of the North Atlantic exhibited an increase in the PCI during the period from 1948 to 2000 (Barton et al. 2003). Barton et al. (2003) showed that the positive PCI trends observed in many areas are similar to the long-term trend in the North Atlantic Oscillation (NAO) index and provided hypotheses about the NAO-dependent physical factors underlying the long-term pattern of phytoplankton variability. Recent studies in fjords reported positive correlations between the NAO and both phytoplankton biomass and the abundance of three species of toxic dinoflagellates (Belgrano et al. 1999). A similar relationship has been shown in the English Channel for diatoms (Irigoien et al. 2000) and *Phaeocystis* sp. abundance (Seuront and Souissi 2002). Barton et al. (2003), however, based their analysis only on yearly mean PCI anomalies, and although the PCI has been shown to be a relevant index of in situ chlorophyll concentration (Batten et al. 2003), it presents several limitations. First, it does not provide relevant information on the structural changes occurring in phytoplankton communities that are likely to influence phytoplankton biomass, and, second, the relation between phytoplankton abundance and biomass is not constant (Hays and Lindley 1994). A first step that would provide further insights into the space–time dynamics of phytoplankton communities is an analysis of diatom and dinoflagellate populations. These data can be used as corollary variables of phytoplankton biomass, allowing comparison of potential differences in the space–time dynamics of the PCI, diatom, and dinoflagellate abundance. Finally, it is also critical to determine how the PCI compares to cell counts and to understand what is causing the observed large increase in phytoplankton biomass with time.

The aim of this study is thus to investigate, over the period extending from 1958 to 2002, (1) the long-term fluctuations of phytoplankton biomass, diatoms, and dinoflagellates; (2) their geographical variation within the North Atlantic basin; (3) their relationship with climate forcing; (4) the contribution of both diatoms and dinoflagellates to the PCI; and (5) the fluctuations of the dominant species over the period of the survey to provide more information on the processes linking climate to changes in the phytoplankton community.

Materials and methods

The sampling—The CPR survey is an upper-layer plankton monitoring program that has regularly collected samples, at monthly intervals, in the North Atlantic and the North Sea since 1946 (Warner and Hays 1994). The CPR is a high-speed sampler, usually towed at 10–18 knots (5–9 m s^{-1}), behind voluntary merchant ships at a standard depth of ca 6.5 m (Hays and Warner 1993). The instrument is powered by an impeller that drives the internal mechanism. Water flows through a 1.62-cm^2 aperture in the CPR nose, down a tunnel where it is filtered through a silk with an average mesh size of 270 μm. The filtering silk is covered by a second layer of silk and reeled into a storage tank filled with 4% formaldehyde (to fix and preserve the plankton). The two bands of silk move continuously across the tunnel at a speed adjusted according to the speed of the ship, via the impeller and gear-box, to 10 cm per 10 nautical miles (18.5 km). Ten centimeters of filtered silk equates to the sampling of 3 m^3 of seawater. After the tow, the CPR is brought back to the laboratory for routine analysis. Methods of counting and data processing have been described by Warner and Hays (1994). Despite the near-surface sampling, studies have shown that this sampling gives a satisfactory picture of the epipelagic zone (Lindley and Williams 1980). The visual estimation of the total phytoplankton biomass, known as the Phytoplankton Color Index (PCI), is determined for each sample. This index has four levels of color from ‘nil’ to ‘green’ (nil: no phytoplankton; very pale green: low biomass of phytoplankton; pale green: medium biomass of phytoplankton; green: high biomass of phytoplankton). These ordinal values have been assigned numerical values based on the work of Colebrook and Robinson (1965). The abundance of each phytoplankton species (or group of species) is estimated by viewing a subsample of each length of the silk, consisting of 20 microscope fields of 0.295 mm in diameter ranged in two diagonals of 10 fields (Robinson and Hiby 1978). One must note here that while the PCI is thought to be a relevant index of in situ chlorophyll concentration, some taxonomic groups—for instance, microflagellates—are not counted in the CPR because their cell wall breaks up in formalin, but they nevertheless contribute to the total PCI.

The data—Most of the diatom and dinoflagellate species have been identified and counted in the same way since 1958. Two taxa—coccolithophores and silicoflagellates—have only been counted since 1993; previously they were merely recorded as being either present or absent. Consequently, only diatoms and dinoflagellates are taken into account in the present work, as they have a complete time series. First, all species identified by the CPR survey (Warner and Hays 1994) and belonging to diatoms or dinoflagellates were grouped by summing the number of cells identified to determine the overall trends of these two groups. Second, diatom and dinoflagellate species with a frequency of occurrence greater than 1% in the samples were used as indicator species to provide more information on the processes linking climate to changes in the phytoplankton community. Five dinoflagellate species (*Ceratium furca, C. fusus, C. horridum, C. lineatum,* and *C. tripos*) and six diatom taxa (*Rhizosolenia alata alata, R. hebetata semispina, R. styliformis*, *Thalassionema nitzschioides*, *Thalassiosira* spp., and *Thalassiothrix longissima*) have thus been investigated further.

The analysis is based on a monthly time series to take into account the effect of seasonal variability. The area of study was divided into six regions, identified through bathymetric criteria and divided according to a North–South axis. The six subregions of the North Atlantic Ocean considered here are as follows (Fig. 1): Northwest (51.5–74.5°N, 79.5–45°W), Southwest (29.5–51.5°N, 79.5–45°W), North Central (51.5–74.5°N, 45–20°W), South Central (29.5–51.5°N, 45–20°W), Northeast (51.5–74.5°N, 20°W–15°E), and Southeast (29.5–51.5°N, 20°W–15°E). In each area, the data obtained for the estimates of phytoplankton biomass (i.e., PCI) and phytoplankton abundance (i.e., total diatoms, total dinofla-

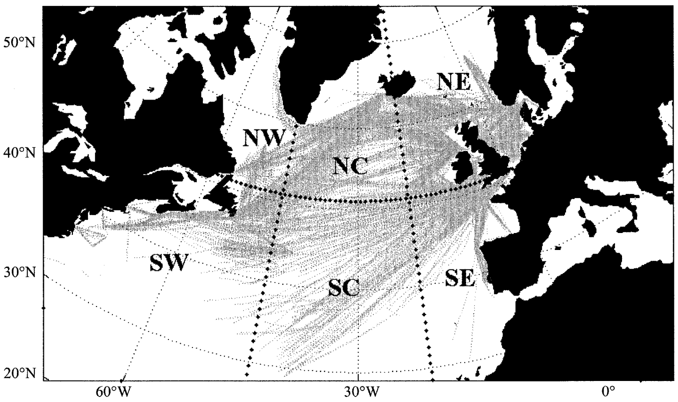

Fig. 1. The North Atlantic basin divided into six regions identified through bathymetric criteria and separated according to a North–South axis: Northwest (NW), Southwest (SW), North Central (NC), South Central (SC), Northeast (NE), and Southeast (SE). CPR samples used in this study are illustrated in gray.

gellates, and indicator species) have been averaged every month over the period ranging from 1958 to 2002; this period was chosen because analytical methodology has been consistent since 1958.

Several indices have been developed to quantify the state of the NAO, but the most widely used is Hurrell's NAO index (Hurrell 1995). This index computes the pressure difference based on measurements from Lisbon, Portugal, and Stykkisholmur, Iceland. In particular, NAO index values averaged from December to March (inclusive) have been used as a climatic index (Hurrell 1995). This index corresponds to the NAO winter index (*see* www.cdg.ucar.edu/~jhurrell/nao.html), which is used in this study. The Sea Surface Temperature (SST; *see* The British Atmospheric Data Center, http://badc.nerc.ac.uk/home) data were used to provide additional climatic information likely to influence phytoplankton growth and abundance.

Statistical analysis—The normality of the data was assessed using a Kolmogorov–Smirnov statistical test. Where data did not correspond to a normal distribution, nonparametric statistics were used for further analysis. The stationarity of time series obtained in each of the six subregions was tested by calculating Kendall's coefficient of rank correlation, τ, between the series and the x-axis values in order to detect the presence of a linear trend. Kendall's coefficient of correlation is used in preference to Spearman's coefficient of correlation, ρ, although the latter was recommended in Kendall (1976), because Spearman's ρ gives greater weight to pairs of ranks that are further apart, while Kendall's τ weights each disagreement in rank equally. We thus eventually de-trended the time series by fitting regressions to the original data by least squares and used the regression residuals in further analysis.

To detect changes, intensity, and duration of any changes in the value of a given parameter, we used the cumulative sums method (Ibanez et al. 1993). The calculation consists of subtracting a reference value (here the mean of the series) from the data; these residuals are then successively added, forming a cumulative function. Successive positive residuals produce an increasing slope, whereas successive negative residuals produce a decreasing slope. A succession of values similar to the mean show no slope.

Autocorrelation was tested on each time series using AutoRegressive Integrated Moving Average; absence of any significant autocorrelation in the hydroclimatic indices ensures the relevance of further statistical analysis between these series and other data (Legendre and Legendre 1998). The relationship between phytoplankton and climate forcing was tested through Spearman correlation analysis performed between the phytoplankton estimators (i.e., abundance of the indicator species, total diatoms, total dinoflagellates, and PCI), the NAO winter index, and SST. This test was conducted between 45 twelve-month series of SST, PCI, total diatom, total dinoflagellate, and indicator species abundance over the period ranging from 1958 to 2002. To test the relationship with the NAO, six time series, from March to August (which correspond to the main period of occurrence of the diatoms and the dinoflagellates), have been correlated with the NAO winter index of the previous winter. In order to infer potential differences in the effect of climate forcing on phytoplankton, correlation analyses were systematically conducted on non–de-trended and de-trended time series.

To identify the phytoplankton group and/or species that contributed to the PCIs in each month over the time period, multiple linear-regression models were constructed on the monthly time series. However, in order to assess complete time series, this analysis has been conducted only on the eastern part of the North Atlantic, which is the most continuously sampled over the study period.

Results

Not enough samples have been obtained in the Northwest area of the North Atlantic over the period from 1958 to 2002 to allow for the relevant application of statistical analysis. No quantitative results are thus available for this area.

Positive global trends have been observed for PCI within the other five subregions of the North Atlantic (Table 1); these trends are significant in the Northeast, Southwest, and South Central for PCI. Total dinoflagellates and *Ceratium furca* have shown a significant positive trend in the South-

Table 1. Results of Kendall's statistical test for the whole time series of Phytoplankton Color Index (PCI), total diatoms, and total dinoflagellates over the period 1958–2002. Significant ($p<0.05$) results are in bold.

	Northeast	Southeast	North central	South central	Southwest
PCI	**0.229**	0.183	0.097	**0.196**	**0.282**
Total dinoflagellates	−0.035	0.040	0.016	0.046	**0.240**
Total diatoms	−0.080	−0.071	−0.049	0.003	0.107

west. Apart from the Southwest Atlantic, where there is a significant positive correlation between SST and both PCI and total dinoflagellates, there is no significant relationship between phytoplankton estimators and the SST. The cumulative sums obtained in the Eastern North Atlantic have shown different phases to the global trends observed with the Kendall's coefficient of rank correlation (Fig. 2). For PCI, there is an initial decreasing phase until 1979 and 1987 in the Southeast and in the Northeast, respectively. Subsequent increases in PCI have been observed. In the Southeast, the increasing trend is stronger than in the Northeast (Fig. 2A). For diatoms (Fig. 2B), there is an initial increasing trend until 1968 in the Northeast and 1970 in the Southeast, then a succession of decreasing trends has been observed. *Thalassionema nitzschioides, Thalassiosira* spp., and *Thalassiothrix longissima* exhibit the same pattern as the one observed for total diatoms. Dinoflagellates (Fig. 2C) exhibit a combination of small-scale fluctuations around a succession of positive and negative phases. The same pattern has been observed for *Ceratium fusus, C. horridum,* and *C. tripos,* which were also the most abundant species in the samples.

Correlation analyses conducted between the 45 year time series of SST, PCI, and phytoplankton species have shown positive relationships across the whole North Atlantic (Fig. 3). However, most significant correlations between SST, PCI, and dinoflagellates (i.e., both total dinoflagellates and indicator species) have been observed in the eastern, rather than the western, part of the North Atlantic Ocean (Table 2). The relationship between SST and diatoms showed a different pattern, as more significant correlations have been observed in the western than in the eastern part of the North Atlantic Ocean for total diatoms as well as for *T. nitzschioides, Thalassiosira* spp., and *T. longissima* (Table 2). Conversely, two of the indicator species (*R. alata alata* and *R. styliformis*) have shown the same pattern as the one observed for dinoflagellates in Northeast and North Central Atlantic. The indicator species that have shown the same pattern as their taxonomic group (i.e., total diatoms) are the species that are the most abundant in the samples: *T. nitzschioides, Thalassiosira* spp., and *T. longissima.*

More detailed analyses of the 12 monthly time series have highlighted that the significance of trends observed for PCI depends on the month and the geographical area (Table 3). Similar results have been found for dinoflagellates and diatoms. In the Northeast and North Central Atlantic, dinoflagellates have shown negative trends (Table 3), while positive trends have been observed in the other regions. On the other hand, positive trends have been observed for total diatoms in the Southwest Atlantic, but trends are negative in the other regions of the North Atlantic (Table 3). Alternatively, in the North Central Atlantic, for total diatoms, significant positive and negative trends have been observed in January and April and from July to October, respectively.

Correlation analyses conducted between the monthly time series and the NAO winter index (Hurrell 1995) have also shown varying results related to time period and study area. Positive relationships have been observed between the NAO and dinoflagellates during April (i.e., total dinoflagellates, *C. furca,* and *C. horridum*) and May (i.e., total dinoflagellates and all indicator species) and between NAO and PCI during April, May, and June in the Northeast Atlantic (Table 4). In the Southeast, NAO and PCI are positively correlated in June and August (Table 4). In the North Central Atlantic, positive

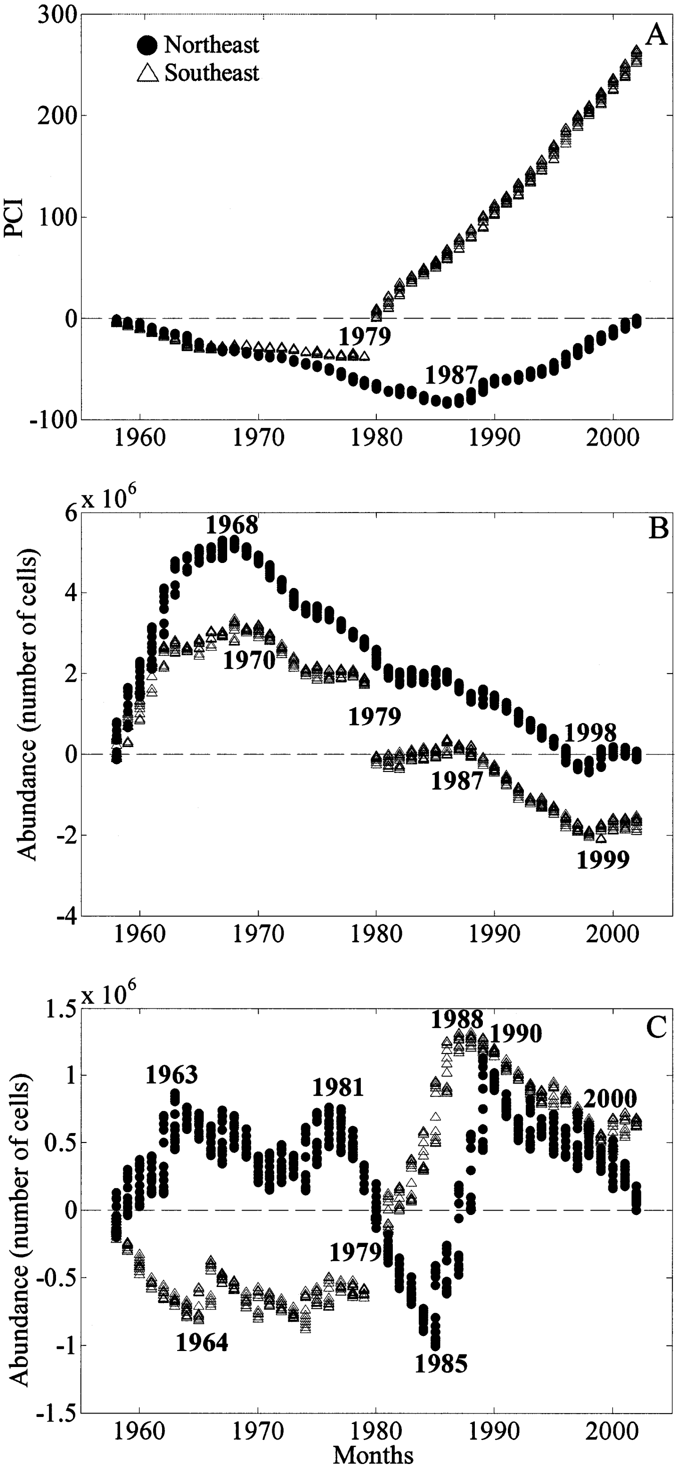

Fig. 2. Cumulative sums of the (A) PCI, (B) total diatoms abundance, and (C) total dinoflagellates abundance for each month over the period ranging from 1958 to 2002 (540 data points) in the Northeast and the Southeast Atlantic.

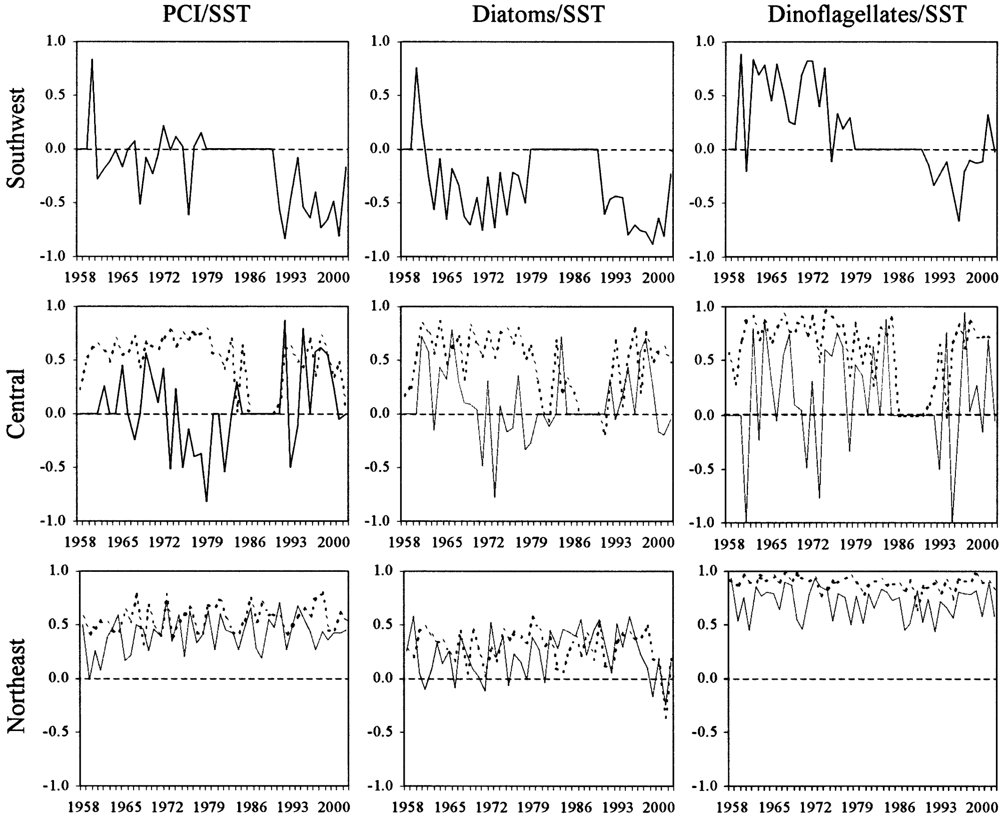

Fig. 3. Fluctuations of the Spearman's correlation coefficient (bold lines) obtained between SST and PCI, total diatoms, and total dinoflagellates over the period ranging from 1958 to 2002 in the Southwest, Central, and Eastern Atlantic. The Central and the Eastern areas have been divided into two parts: North (dashed line) and South (solid line).

relationships have been observed between NAO and PCI in May and June, even though diatoms and NAO are negatively correlated in July (i.e., total diatoms, *Thalassiosira* spp., and *T. nitzschioides*) and August (i.e., total diatoms and *T. nitzschioides*) and positively correlated in May (i.e., total diatoms, *R. hebetata semispina, Thalassiosira* spp., and *T. longissima*) and June (i.e., total diatoms, *R. hebetata semispina,* and *Thalassiosira* spp.). In the South Central area, the NAO shows a positive relationship with PCI in April and July, with diatoms in April and a negative relationship with dinoflagellates in June (i.e., total dinoflagellates, *C. fusus*, and *C. lineatum*). In the Southwest, positive relationships have been observed between the NAO and PCI in April and May (Table 4), with dinoflagellates in April (i.e., total dinoflagel-

Table 2. Significant correlations (%) over the period 1958–2002 between the monthly time series of Phytoplankton Color Index (PCI), dinoflagellates, and diatoms and SST across the North Atlantic.

	Northeast	Southeast	North central	South central	Southwest
PCI	64.44	28.89	53.33	17.78	17.78
Total dinoflagellates	100	88.89	68.89	31.11	22.22
Ceratium furca	100	64.44	46.67	20	4.44
Ceratium fusus	100	80	60	15.56	31.11
Ceratium horridum	97.78	44.44	28.89	0	8.89
Ceratium lineatum	100	46.67	44.44	2.22	6.67
Ceratium tripos	100	91.11	33.33	13.33	8.89
Total diatoms	4.44	11.11	53.33	15.56	33.33
Rhizosolenia alata alata	95.56	71.11	31.11	2.22	6.67
Rhizosolenia hebetata semispina	4.44	24.44	13.33	0	4.44
Rhizosolenia styliformis	75.56	24.44	51.11	0	8.89
Thalassionema nitzschioides	17.78	13.33	37.78	2.22	31.11
Thalassiosira spp.	0	2.22	33.33	8.89	26.67
Thalassiothrix longissima	35.56	22.22	48.89	4.44	37.78

Table 3. Results of Kendall's statistical test for the monthly time series of (A) Phytoplankton Color Index (PCI), (B) total diatoms, and (C) total dinoflagellates over the period 1958–2002. Significant ($p<0.05$) results are in bold.

	Northeast			Southeast			North central			South central			Southwest		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Jan	**0.362**	0.101	−0.125	**0.446**	0.130	0.097	**0.337**	**0.289**	0.223	−0.099	0.053	0.145	**0.370**	**0.394**	**0.362**
Feb	**0.339**	0.122	−0.079	**0.353**	−0.070	−0.087	**0.249**	0.196	0.192	**0.252**	0.154	0.089	**0.424**	**0.397**	**0.382**
Mar	0.145	−0.203	−0.029	0.187	−0.200	0.197	**0.249**	0.019	0.172	**0.229**	−0.010	0.053	**0.344**	**0.391**	**0.412**
Apr	**0.298**	−0.074	0.108	**0.251**	−0.126	0.190	0.102	−0.097	0.214	**0.267**	0.226	0.180	**0.354**	0.212	**0.465**
May	**0.434**	**−0.351**	0.087	**0.226**	−0.105	0.187	−0.088	−0.165	−0.185	0.219	0.136	**0.276**	0.124	0.032	**0.301**
Jun	**0.509**	**−0.210**	0.067	**0.516**	0.106	0.090	0.019	−0.190	0.081	0.102	**−0.261**	−0.155	0.151	−0.056	**0.374**
Jul	**0.313**	**−0.250**	−0.059	**0.485**	−0.163	0.048	0.12	**−0.383**	**−0.228**	**0.384**	0.006	0.179	0.210	0.037	0.144
Aug	**0.547**	**0.224**	0.040	**0.542**	−0.171	0.157	0.184	**−0.307**	−0.177	0.278	0.124	0.277	**0.312**	0.237	−0.084
Sep	**0.378**	−0.177	**−0.348**	**0.361**	**−0.212**	**0.204**	−0.08	**−0.344**	**−0.214**	0.236	−0.091	0.153	**0.304**	−0.008	0.028
Oct	0.197	**−0.296**	**−0.444**	0.131	−0.181	−0.119	**0.307**	−0.142	0.022	0.171	0.004	0.038	0.243	−0.028	0.039
Nov	**0.281**	−0.038	**−0.271**	0.162	**−0.230**	−0.104	0.121	−0.053	−0.013	**0.493**	−0.215	0.192	**0.494**	0.246	0.153
Dec	**0.409**	0.003	−0.084	**0.339**	−0.021	−0.016	**0.361**	0.192	0.179	0.214	0.113	−0.062	**0.489**	0.228	**0.246**

Table 4. Results of Spearman's correlation analysis between the monthly time series of Phytoplankton Color Index (PCI), diatoms, and dinoflagellates and the NAO winter index over the period 1958–2002. Significant ($p<0.05$) results are in bold.

	PCI					Diatoms					Dinoflagellates				
Months	Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug
Northeast	**0.338**	**0.371**	**0.482**	0.176	0.234	0.074	**−0.259**	−0.027	−0.131	−0.109	**0.389**	**0.546**	0.109	0.084	−0.139
Southeast	0.172	0.218	**0.295**	0.189	**0.297**	−0.008	0.078	0.070	−0.146	0.042	0.207	0.183	0.039	0.070	0.143
North central	0.010	**0.408**	**0.380**	0.029	0.146	−0.210	**0.272**	0.213	−0.274	**−0.356**	0.025	0.182	0.111	−0.143	−0.139
South central	**0.285**	0.237	0.029	**0.331**	0.195	**0.300**	0.242	−0.144	−0.134	0.030	0.191	0.202	**−0.360**	0.046	0.025
Southwest	**0.328**	**0.395**	−0.015	0.249	0.145	0.076	0.137	−0.110	0.080	**0.281**	**0.368**	0.178	**0.418**	−0.151	−0.148

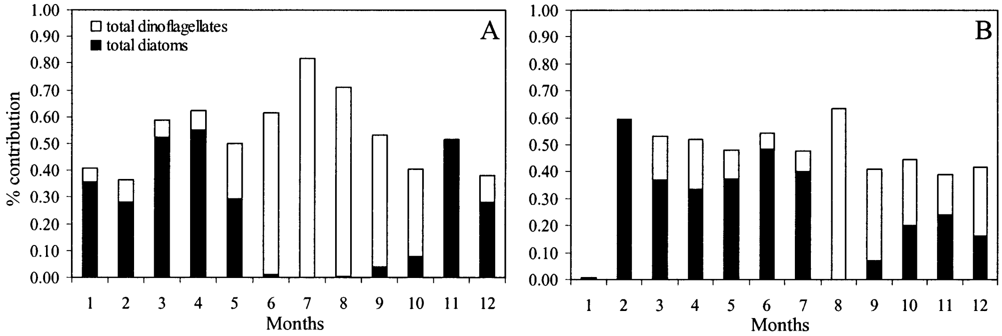

Fig. 4. Contribution to the PCI of total diatoms and total dinoflagellates in the (A) Northeast and (B) Southeast Atlantic.

lates, *C. lineatum,* and *C. tripos*) and June (i.e., total dinoflagellates) and with diatoms in August (i.e., total diatoms, *R. alata alata, R. hebetata semispina,* and *T. nitzschioides*). The analyses conducted on the de-trended time series led to similar results, but only during the spring, as no significant correlations were observed for other months.

Finally, Fig. 4 displays the results of the multiple linear regressions conducted on the monthly time series to identify the contribution of diatom and dinoflagellate to the PCI in the Eastern Atlantic. This contribution is variable depending on the month. In the Northeast Atlantic, the main contribution of diatoms occurs between January and May and during November and December (Fig. 4). For the dinoflagellates, the main contribution is between June and October (Fig. 4). In contrast, in the Southeast Atlantic, the contribution of diatoms and dinoflagellates to PCI is more variable over the whole year. The main contribution of diatoms to the PCI thus occurred from February to July and in November and from August to October and in December for the dinoflagellates (Fig. 4). No significant contribution of diatoms and dinoflagellates to the PCI has been identified in January.

Discussion

In the North Atlantic Ocean, between 1958 and 2002, there are evident overall trends of increasing phytoplankton color and dinoflagellates and a decrease of diatoms. This increasing trend of the PCI has already been shown in the North Sea (Reid and Edwards 2001), in the area west of the British Isles (Edwards et al. 2001), over the Scotian Shelf and Georges Bank in the Northwest Atlantic (Sameoto 2001), and recently over all the North Atlantic basin (Barton et al. 2003). In the framework of this study, the use of diatoms and dinoflagellates allowed for a better understanding of the processes leading to the global trends observed for the PCI.

Phytoplankton variability in the Eastern Atlantic: Toward sea surface temperature and nutrient control—In the Southern North Sea, the increase in phytoplankton biomass has been attributed to an increase in nutrient inputs from the major European rivers during the past decades (Richardson 1997). However, eutrophication mainly has an effect on phytoplankton biomass in the coastal margins and, in particular, those areas that have a limited water exchange (Edwards et al. 2001). In the offshore waters of the North Sea, variability in environmental conditions is thought to play a dominant role in temporal fluctuations of phytoplankton biomass (Edwards et al. 2001). In this study, the Northeast Atlantic area brings together different types of environments, such as the North Sea, the English Channel, the Celtic Sea, the Irish Sea, and the area west of the British Isles (which corresponds to oceanic waters). In such open waters, eutrophication cannot really explain the fluctuations in phytoplankton biomass.

It is possible, however, to relate phytoplankton fluctuations to the hydrometeorological processes characterizing the Northern hemisphere. These processes are thus likely to control those physical parameters that are likely to affect phytoplankton growth (e.g., temperature and turbulence). Temperature determines the rate at which phytoplankton cells divide and at which nutrient supply and wind-induced turbulent mixing control the onset of the spring phytoplankton bloom (Sverdrup 1953). All these parameters have also been shown to be influenced by the NAO, the atmospheric variables exerting strong forcing on the ocean, leading to changes in sea surface temperature, seawater salinity, vertical mixing, circulation patterns, and in northern areas, ice formation (Visbeck et al. 2003).

More specifically, the present work showed that the relationship between PCI, dinoflagellates, diatoms, and the SST varies depending on the area, there being a stronger relationship between SST and PCI or dinoflagellates in the Eastern part of the ocean (*see* Table 2). The inverse has been observed for diatoms (i.e., *T. nitzschioides, Thalassiosira* spp., and *T. longissima*), with a stronger correlation in the Western Atlantic. These observations can be linked to the influence of the NAO through the North Atlantic basin, as Drinkwater et al. (2003) have shown that the physical response to NAO forcing varies spatially across the North Atlantic. Furthermore, the main factors likely to affect phytoplankton dynamics and community structure (besides light, temperature, and salinity) are turbulence and the related nutrient supply (Rodriguez et al. 2001; Li 2002).

Different adaptive strategies are required to deal with different combinations of these factors, embodied mainly in the differences between diatoms and dinoflagellates (Margalef 1973). Dinoflagellates possess an undulating flagellum that keeps the cell turning and accelerates the flow of water over the cell body, which improves the chances for nutrient absorption (Margalef 1997). In stratified and low turbulent water, it pays to invest energy in swimming and so to be able to position the cell in the most favorable environment. This optimization can be useless in turbulent water, where the nutrients are more easily redistributed in the water column and where nonmotile diatoms flourish frequently. So in nutrient-depleted stratified water, dinoflagellate species may be dominant; conversely, in turbulent and nutrient-rich water, diatom species would be dominant. Warmer surface temperatures related to the increasing NAO winter index promote earlier, or more intense, stratification of the upper water column (Drinkwater et al. 2003). According to Margalef's (1973) hypothesis, all these factors would create an environment favoring the growth of dinoflagellates (e.g., *C. tripos,* a typical species of mixed Atlantic waters) over the growth of diatoms (e.g., *R. styliformis*) in both parts of the eastern North Atlantic. This is fully congruent with our observations regarding the differential relationships found between dinoflagellates, diatoms, and the NAO (*see* Tables 3, 4).

Phytoplankton fluctuations in the Western Atlantic: Basin-scale circulation control—Bathymetry, coupled with the differences in the relative strength and/or seasonality of advection, tidal mixing, and stratification, lead to a strong spatial heterogeneity in the oceanographic environment that phytoplankton encounter in the Gulf of Maine (Thomas et al. 2003). Georges Bank, on the other hand, remains relatively well mixed vertically throughout the year, eliminating much of the influence of stratification on the timing of phytoplankton seasonality (Thomas et al. 2003). In this study, PCI, dinoflagellates, and diatoms have all shown significant increasing trends in this area but during different periods. Diatoms have shown an increase between January and March, and dinoflagellates increased in spring. These observations correspond to an increase in the occurrence of these two taxa during the first months of the period in which they are usually present, leading to an earlier appearance of these taxa during the year. Similar conclusions have been drawn for the dinoflagellates in the Northeast area. Furthermore, positive relationships have been observed between the winter NAO and spring values for both dinoflagellate (i.e., *C. lineatum* and *C. tripos*) and the PCI and, on the other hand, the diatoms (i.e., *R. alata alata, R. hebetata semispina,* and *T. nitzschioides*) during August.

Thomas et al. (2003) suggested that basin-scale forcing associated with the NAO, through its influence on hydrographic structure, also has the potential to induce interannual variability in phytoplankton dynamics in the Gulf of Maine. During positive NAO phases, this area is subjected to warmer, drier, and milder conditions (Hurrell 1995; Visbeck et al. 2003). The NAO also affects the shallow and deep-water circulation patterns of the North Atlantic. During positive phases of the NAO, convection is deeper and more intense in the Labrador Sea, and a relatively cool, fresh, and thick layer of Labrador Sea Water is formed (Dickson et al. 1996). This results in higher salinity and temperature on the Scotian Shelf and in the Gulf of Maine (Petrie and Drinkwater 1993) and in higher nutrient concentrations (Gatien 1976). The observed increase of the PCI can then be linked to the increase in nutrients in the Gulf of Maine and the Scotian Shelf. Higher salinity and temperature associated with higher nutrient concentration can also create favorable conditions for the growth of dinoflagellates such as *C. lineatum* and *C. tripos,* which are typical of mixed Atlantic waters, in spring. Diatom species typical of oligotrophic waters, such as *Rhizosolenia* spp., thus encounter favorable conditions at the end of the summer, when low nutrient conditions prevail.

Phytoplankton changes in the central Atlantic: Meteorological control—Few studies have focused on the central part of the North Atlantic Ocean (Kushnir et al. 1997; Hurrell et al. 2003). Here, we observed long-term increasing trends in PCI over the whole central Atlantic area and only in the South Central area for dinoflagellates. In contrast, positive then negative trends have been observed for diatoms in the North Central area (Table 3). These observations correspond to a decrease in the occurrence of this taxa during the last months of its bloom period, leading to a decrease in its presence during the year and/or to an earlier bloom. The same situation has been observed for the dinoflagellates in the South Central area. Their abundance at the beginning of the bloom significantly increased, indicating an earlier presence of dinoflagellates during the year. In addition, the relationship between NAO and phytoplankton is clearly different, whether it relates to different taxonomic groups or to PCI. A positive relationship has been observed between both PCI and diatoms (i.e., *R. hebetata semispina, Thalassiosira* spp., and *T. longissima*) and NAO in the north and south of the area. On the contrary, a negative relationship has been identified in the North Central area between diatoms (i.e., *T. nitzschioides,* a typical species in the Central Atlantic Ocean) and NAO in August and between dinoflagellates (i.e., *C. fusus* and *C. lineatum*) and NAO in June in the South Central (*see* Table 4).

While it is still difficult to clearly identify the processes driving the patterns discussed above, it should be noted that changes in the mean circulation patterns over the North Atlantic associated with the NAO are also associated with changes in the intensity and number of storms. During winter, a well-defined storm track connects the North Pacific and North Atlantic basins, with maximum storm activity over the oceans (Hurrell et al. 2003). As the ocean integrates the effects of storms in the form of surface waves, the recent upward trend toward more positive NAO index winters could be associated with increased wave heights over the northeast Atlantic and decreased wave heights south of 40°N (Kushnir et al. 1997). As the increase in storms will lead to an increase in wind-induced vertical mixing, during positive NAO phases, a larger area in the center of the North Atlantic is expected to be less stratified and cooler than normal. As these parameters strongly influence phytoplankton growth and species succession, it is believed that their complex interactions might play a role in the timing and temporal patterns of diatom and dinoflagellate occurrence, abundance, and succession. Further information relating to the specific hydrometeorological conditions characterizing our sampling would nevertheless be necessary to infer the previous hypothesis.

Differential contribution of phytoplankton taxonomic groups to the PCI—In the Northeast Atlantic, the main contributors to the PCI are diatoms (i.e., *Thalassiosira* spp. and *T. longissima*) between January and May and dinoflagellates (i.e., *C. furca* and *C. fusus*) between June and October. These periods correspond to the characteristic bloom periods of these groups. However, while from March to September, and in November, 52% to 82% of the PCI can be explained, respectively, by the contribution of diatoms and dinoflagellates, during other months they explain only up to 40% of the PCI (Fig. 4). The same pattern occurs in the Southeast area, where 39% to 64% of the PCI is explained by diatoms and dinoflagellates, respectively, between February and December. Diatoms (i.e., *R. alata alata*, *T. nitzschioides,* and *Thalassiosira* spp.) and dinoflagellates (i.e., *C. furca* and *C. tripos*) are the main contributors to the PCI between February and July and between August and December, respectively, in the Southeast. During January, only 1% of the PCI is explained by these groups (Fig. 4). Other categories of phytoplankton must therefore also be involved in the fluctuations of the PCI. Other taxa identified by the CPR survey have not been taken into account in this study, and some taxa are too small to be counted and identified by the CPR survey. Microflagellates, for instance, would not be identifiable in the CPR samples, as they disintegrate in formalin, but their chloroplasts would survive to add to the coloration of the silks. Future studies would then benefit from more in-depth investigations of the relative contribution of other taxonomic groups identified by the CPR survey to the PCI, in order to improve the ecological relevance of this index.

Finally, we stress that despite the changes observed in diatom and dinoflagellate abundance in relation with NAO and/or SST, no change has been observed in the species composition, which reflects the stability of the phytoplankton dynamics. More specifically, our results are fully congruent with previous work by Rodriguez et al. (2001) and Li (2002) and Hallegraeff (1993), showing, respectively, the importance of shifts in the phytoplankton assemblages in relation to mixing/stratification regimes, large-scale advection and small-scale turbulence, and an apparent global increase in harmful algal blooms (mainly dinoflagellate species). This study demonstrates that there is an indirect impact of the NAO on phytoplankton dynamics, via physical factors like temperature, wind-induced mixing, or currents. It is, however, still difficult to explain unambiguously all the mechanisms involved in the control of the observed patterns in phytoplankton biomass at this scale. In the present work we used six subregions of the North Atlantic Ocean that are considered to be representative of significantly different types of environments. However, because local variability in environmental conditions is thought to play a dominant role in temporal fluctuations of phytoplankton biomass (Hasegawa et al. 2004), future studies could take advantage of defining smaller areas within these subregions to study more precisely the processes influencing the long-term variation of phytoplankton assemblages.

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