

Distribution of dinoflagellate cysts in surface sediments of the northern North Atlantic in relation to nutrient content and productivity in surface waters

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Received 30 July 1999; accepted 13 January 2000

Abstract

Analyses of dinoflagellate cyst assemblages from the surface sediments of 371 sites from the North Atlantic Ocean were performed in order to define relationships with nitrate, phosphate, silica and productivity in the upper water layer. Statistical analyses reveal close links between dinocyst assemblages and nitrate content in February that provide a measurement of nitrate availability. Amongst the taxa in the assemblages, *Nematosphaeropsis labyrinthus*, which positively correlates with nutrients, shows an eutrophic relationship, whereas *Impagidinium aculeatum*, *Impagidinium patulum*, *Spiniferites ramosus*, *Spiniferites mirabilis* and *Lingulodinium machaerophorum* have a rather oligotrophic relationship. On these grounds, transfer functions were tested using multiple regressions and the best analogue technique to reconstruct nitrate content. Both methods yielded reasonable estimates and allow the reconstruction of the nitrate concentrations in February with an accuracy better than $1.45 \mu\text{mol m}^{-3}$. At the scale of the study area, there are also tenuous links between the dinocyst assemblages and productivity. Transfer functions were tentatively tested for the reconstruction of annual productivity and yield estimates with an accuracy of about $26.5 \text{ gC m}^{-2} \text{ year}^{-1}$. These results demonstrate that dinocyst assemblages can be used for the reconstruction of productivity and nitrates. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Dinocyst; Nitrate; North Atlantic; Nutrient; Palynology; Productivity

1. Introduction

During the last decade, many attempts to reconstruct changes in biological productivity and carbon fluxes in the ocean based on sedimentary records have been published (e.g. Shackleton et al., 1983; Sarnthein and Winn, 1988; Mix, 1989; Pedersen et al., 1991; Farrell et al., 1995; Ganeshram et al., 1995; Haug et al., 1998; Knies and Stein, 1998). Most of the

approaches used for the estimation of the biogenic uptake and fluxes rely on geochemical measurements in buried organic matter (e.g. Corg, C/N, ^{15}N , ^{13}C). However, the biogenic signal in sediment is often difficult to interpret because of diagenetic processes affecting the organic matter during its settling through the water column, within the nepheloid layer, and in the reactive mixed layer below the sediment–water interface (Müller and Suess, 1979; Meyers, 1994). The organic carbon fluxes and the isotopic composition of organic compounds in the sediments also appear to be a complex function of the allochthonous inputs through currents and lateral transport (Knies

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and Stein, 1998), autochthonous biological productivity in the upper water layer, fluxes through the water column, sediment accumulation rates (Ingall and Van Cappellen, 1990), oxygen availability in the sediment–water interface, and from other sources (Pedersen and Calvert, 1990; Canfield, 1994). Here we propose an original approach for the reconstruction of nutrient and productivity from sedimentary records based on organic-walled dinoflagellate cysts (or dinocysts), that are composed of refractory organic compounds (Loeblich and Loeblich, 1984; Evitt, 1985). We hypothesize that the dinocysts may provide a picture of biogenic fluxes that is independent from the diagenetic processes undoubtedly taking place in sediments.

Dinoflagellates, together with diatoms and coccolithophorids, represent a major part of the primary production in marine environments (e.g. Parsons et al., 1984). They also represent the major part of the primary producers recorded in the sediment. During their life cycle, when the number of cells reaches a maximum in the water column, dinoflagellates undergo sexual reproduction that produces hypnozygotes for a resting phase of variable duration. The hypnozygote of many dinoflagellate species (about 10–15%) is protected by a highly resistant organic-walled cyst (e.g. Dale, 1976; Head, 1996). These cysts are fossilisable and routinely recovered in palynological preparations and constitute a fragmentary picture of the original dinoflagellate populations. Several studies of dinocyst assemblages on the sea floor has led to the documentation of their distribution in relation with hydrographical parameters such as temperature and salinity (Harland, 1983; Turon, 1984; Mudie and Short, 1985; de Vernal and Giroux, 1991; Edwards and Andrieu, 1992; Matthiessen, 1995; Marret and de Vernal, 1997; Rochon et al., 1999). The relationships between absolute cyst abundance or taxa percentages, and the productivity or nutrients were also proposed on empirical grounds by several authors (e.g. Turon and Londeix, 1988; Lewis et al., 1990; de Vernal et al., 1992; Powell et al., 1992; Dale and Fjellså, 1994; Hillaire-Marcel et al., 1994; Marret, 1994; Zonneveld, 1996).

In order to explore further the links between dinocyst assemblages in surface sediments, and both nutrient content and productivity, we used a modern dinocyst database representative of the northern North

Atlantic and adjacent basins (de Vernal et al., 1997; Rochon et al., 1999). This database has already led to the demonstration of close relationships between the dinocyst assemblages and some hydrographic parameters, including the temperature of the warmest and coldest months (i.e. August and February), salinity and seasonal extent of sea–ice cover. Here we hypothesize that nutrients and productivity also exert a determinant control on dinocyst distribution. Most dinoflagellates are photosynthetic and constitute tracers of primary productivity. The dinocyst assemblages also include the cyst of heterotrophic taxa that are feeding on other primary producers such as diatoms (Jacobson and Anderson, 1986; Schnepf and Elbrachter, 1992; Jacobson and Anderson, 1996). This is especially the case for taxa belonging to the family of Congruentidiaceae (cf. Fensome et al., 1993) that appear to be relatively abundant in diatom rich waters (Dale, 1996; Harland and Pudsey, 1999). Thus, the overall dinocyst population preserved on the sea floor may provide an image of primary production as a whole.

With the aim to evaluate the interdependency between dinocysts and both primary productivity and nutrients, we have used the above mentioned dinocyst database (Fig. 1) and have compiled a nutrient database including nitrate, phosphate and silica concentrations from the National Oceanographic Data Center (NODC, 1994) for each reference site. We have also extracted productivity data estimated from satellite measurements (Feldman et al., 1989; Antoine and Morel, 1996; Antoine et al., 1996). Different statistical analyses have been performed on these data in order to understand the environmental factors controlling the distribution of the dinocyst taxa and assemblages. Finally, transfer functions for the reconstruction of paleonutrients and paleoproductivity have been tested.

2. Material and methods

2.1. The palynological data

The dinocyst data (Figs. 1 and 2a) result from analyses of surface sediment samples (0–1 cm) collected mainly by box-coring or gravity coring in the northern North Atlantic and its adjacent basins (cf.

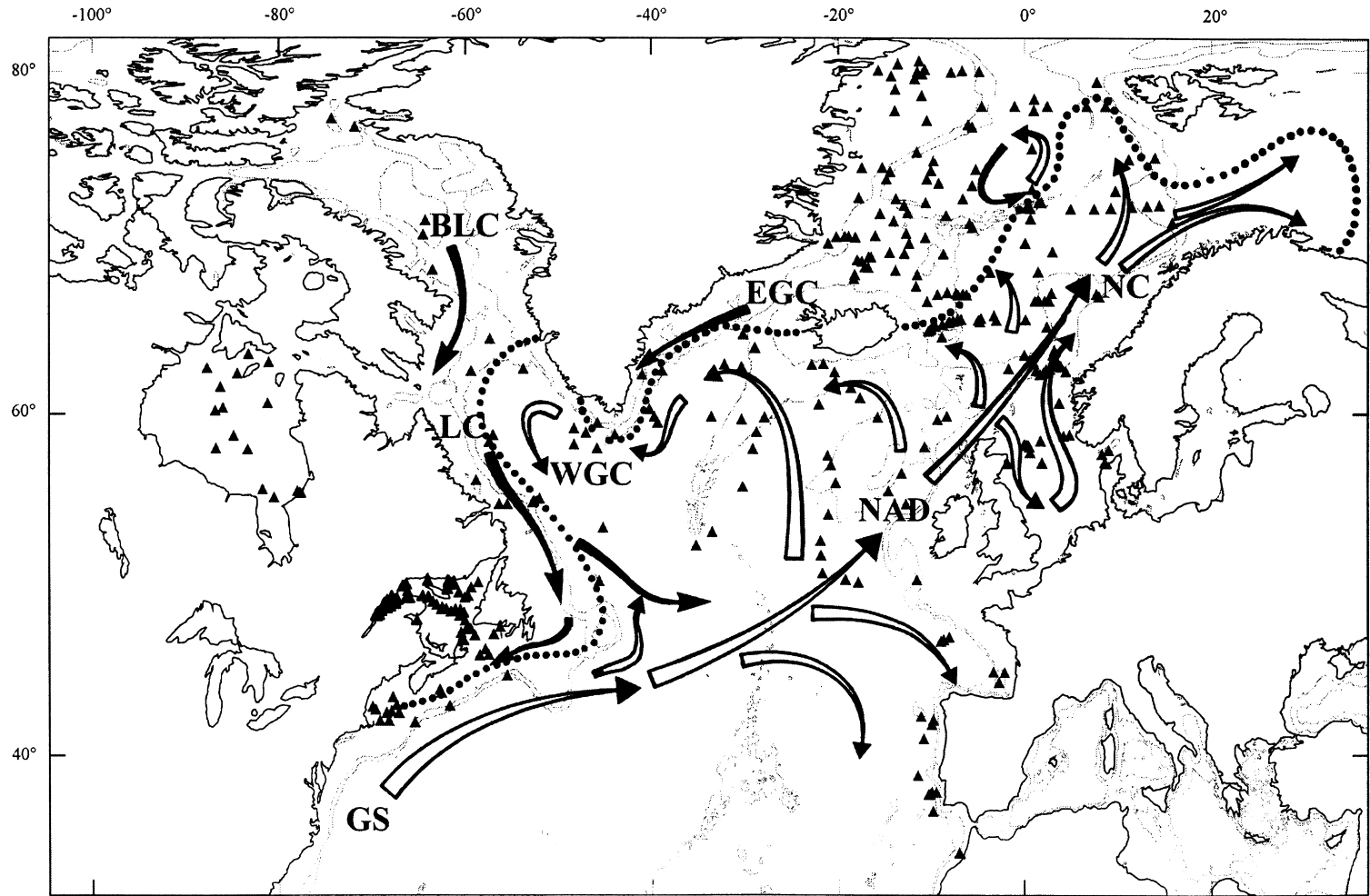


Fig. 1. Map of the northern North Atlantic Ocean. The triangles show the location of surface sediment samples used to develop the reference database of dinocyst assemblages (de Vernal et al., 1997; Rochon et al., 1999). In addition to the sites shown, there are 19 others from the Barents Sea. The isobaths indicate water depths of 500 and 2000 m. The dotted line is the southern limit of winter sea-ice (spanning more than one month per year on the average; compilation of the 1953–1990 data set provided by the National Climate Data Center in Boulder, Colorado). The cold currents are illustrated with black arrows as follows: BLC = Baffin Land Current; LC = Labrador Current; EGC = East Greenland Current. Open arrows illustrate the warm currents, which include the Gulf Stream (GS) and the North Atlantic Drift (NAD), in addition to their westward and eastward branches (WGC = West Greenland Current; NC = Norwegian Current).

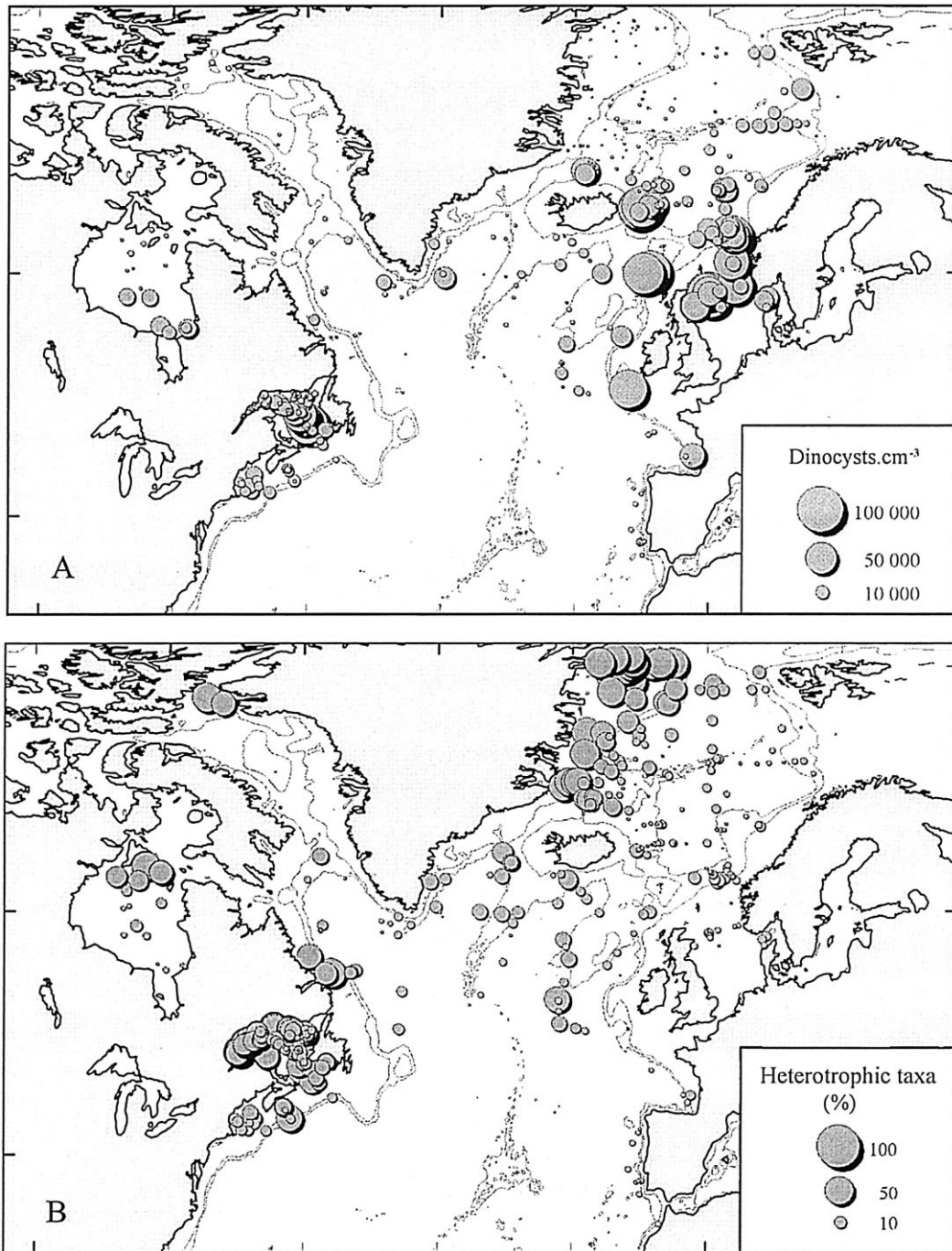


Fig. 2. Distribution maps of dinocyst assemblages in surface sediment samples of the northern North Atlantic: (A) dinocyst concentrations per unit of volume (cubic centimeters) of wet sediment; (B) percentage of heterotrophic taxa including *Brigantedinium* spp., *Selenopemphix quanta*, *Trinovantedinium capitatum* and *Polykrikos schwartzii*. *Algidasphaeridium?* *minutum* which has uncertain affinities is also included as an heterotrophic taxon.

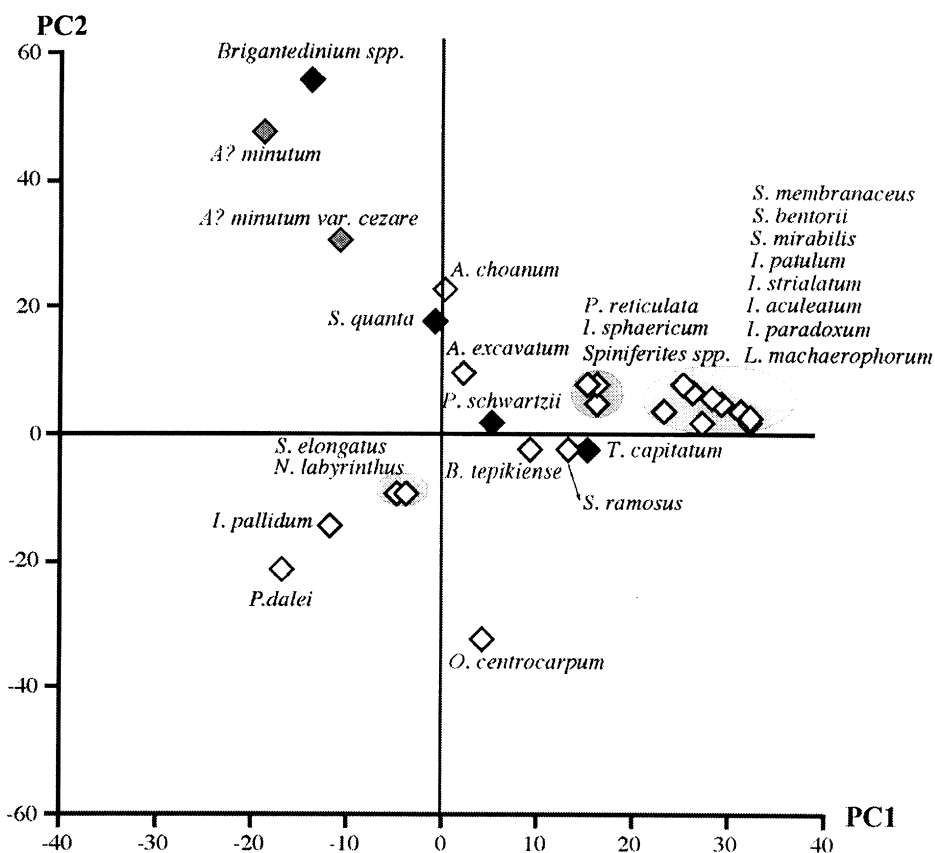


Fig. 3. Weighting of dinocyst taxa in the assemblages after principal component analyses. The black diamonds are heterotrophic taxa whereas the gray diamonds correspond to taxa with uncertain taxonomic affinities, but believed to be heterotrophic. The open diamonds correspond to taxa known as autotrophic.

Rochon et al., 1999). These samples are assumed to be recent, but may represent 10^1 – 10^3 years depending upon sedimentation rates and biological mixing. For example, the surface sediment collected at some sites of the St. Lawrence estuary represents the last decade (e.g. Mekireche-Telmat, 1997), whereas sediments represent the last millennia in many offshore stations of the Labrador Sea (e.g. Rochon and de Vernal, 1994). These “modern” assemblage, representing different time intervals, may constitute a source of error when comparing the dinocyst data to “modern” oceanographic data obtained through instrumental measurements.

The laboratory treatment procedures and the systematics, that were standardized in order to establish a consistent database, are described by de Vernal et al. (1993, 1994, 1997) and Rochon et al. (1999). It is

of note that there are two independent classifications for organic-walled cysts and thecal stage (cf. Head, 1996 for the cyst vs. theca taxonomic equivalence). Here we are using a paleontological nomenclature that corresponds to the cyst stage (cf. systematics section in Rochon et al., 1999). The dinocyst database, that includes 371 reference sites, comprises a total of 27 taxa after elimination of rare taxa and grouping of some species (Rochon et al., 1999). The assemblages include mainly autotrophic taxa, together with a few heterotrophic taxa (Figs. 2b and 3). Thus, two different methods were used to calculate taxa percentages in the assemblages in order to perform statistical analyses:

- (i) in the ‘D-27’ data set, most taxa including the cyst of autotrophic and heterotrophic dinoflagellates were considered;

- (ii) in the 'D-20' data set, the cysts of heterotrophic taxa were discarded (i.e. *Brigantedinium* spp., *Selenopemphix quanta*, *Trinovantedinium capitatum* and *Polykrikos schwartzii*. *Algidaphaeridium? minutum* has uncertain affinities but is included as an heterotrophic taxon). D-27 data set include 371 sites and D-20 data set include 359 sites (some sites were excluded from the D-27 data set because they include only heterotrophic taxa).

2.2. The physico-chemical data

Nitrate (NO_3^-), phosphate (PO_4^{3-}) and silica (SiO_2) data are from the World Ocean Atlas data set published by the NODC (1994). Additional data for the Gulf and Estuary of St. Lawrence and the Labrador Sea were provided by Environment Canada. Queries of environmental data were performed using an ORACLE relational database management system.

Compilations were made of the calculation of mean nutrient concentrations in surface water masses (0–20 m depth) within areas defined by a radius of 60 nautical miles at most locations, and by a radius of 30 nautical miles at the nearshore stations (i.e. in the Gulf and Estuary of the St. Lawrence, and in the Skaggeak Strait); We used the monthly means of nutrients in February and August. These months were selected because more nutrient data are available for February and August than for any other months. These two months also represent distinct and extreme hydrographical conditions inasmuch as they correspond to the coldest and the warmest months of the annual cycle respectively. Furthermore, February constitutes a month with extremely low productivity, especially in areas covered by seasonal sea-ice (Antoine and Morel, 1996) and maximum mixing due to cooling and density increase in the upper water layer that fosters vertical convection (Lewis et al., 1986; Brown et al., 1989).

The nutrient data set was filtered in order to eliminate some values that are questionable because of sparse measurements and/or too scattered data. Monthly averages based on less than three measurements were excluded. Values having a standard deviation larger than the mean by more than 200% were also considered unreliable. Particularly large standard deviations, which led to exclusion of sites,

were observed in coastal areas where there is high spatial and temporal heterogeneity. After filtering, the overall nutrient database includes 85 to 213 reference points depending upon the respective nutrient and the month considered (Fig. 4). The limited data, and the relatively large standard deviations, that reflect a high interannual variability and/or variable accuracy of measurements, constitute potential sources of error.

2.3. The productivity data

Productivity data are from remote sensing analyses as published by Antoine et al. (1996) and Antoine and Morel (1996). The data represent estimates of the column-integrated oceanic primary productivity calculated from chlorophyll-like pigment concentrations. The integrated water column represents approximately 1.5 times the euphotic zone, depending on the area considered (Antoine et al., 1996). The data were obtained with sea-color observations compiled from Coastal Zone Color Scanner (CZCS), an instrument fixed on the NASA satellite Nimbus 7, between November 1978 and June 1986 (Antoine and Morel, 1996; Feldman et al., 1989).

The original data are reported on a 1/5 degree grid scale. Queries were performed using an ORACLE relational database management system for an area of 1/2 degree around the sites. The annual productivity measurements have an almost continuous coverage and data are available for 362 of the 371 sites (Fig. 5). However, uncertainties concerning the accuracy of satellite measurements and thus the net primary productivity estimates are of the order of 17% (Antoine and Morel, 1996).

2.4. Statistical treatments of the data and transfer function

In order to understand the distribution of dinocysts and to determine which parameters control their distribution, principal component (PC) analysis was performed on the D-27 and D-20 data sets with software developed by Guiot (1990). Logarithmic transformation was done on taxa percentages in order to enhance the weight of accompanying taxa (cf. de Vernal et al., 1993).

Other statistics include Pearson's correlation on a matrix that comprises the percentages of dinocyst taxa

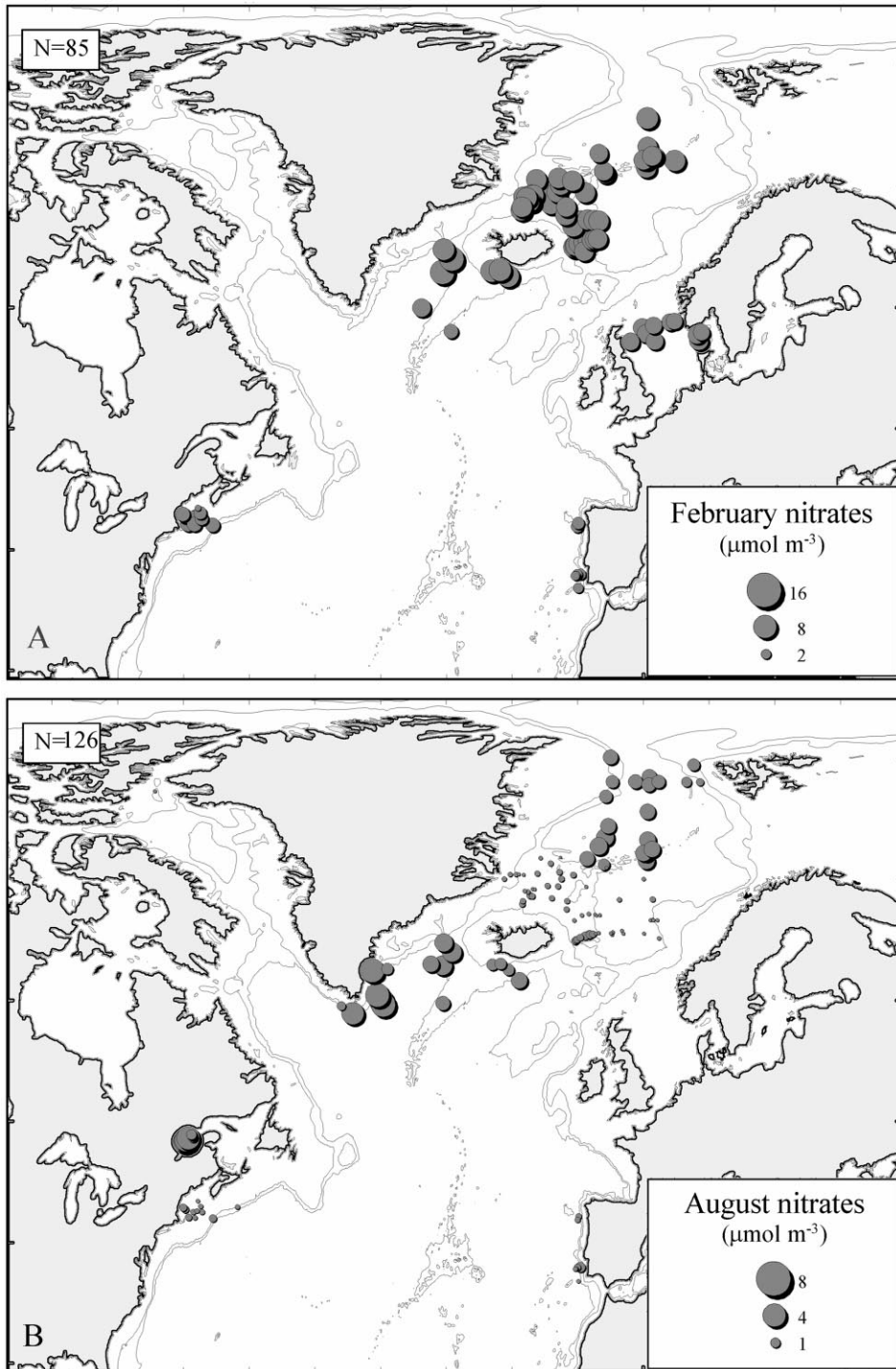


Fig. 4. Distribution maps of nutrient concentrations in surface waters (0–20 m) expressed in $\mu\text{mol m}^{-3}$. The number N in the top left of the maps corresponds to the number of data points available from the NODC (1994) data set: (A) Nitrate in February; (B) Nitrate in August; (C) Phosphate in February; (D) Phosphate in August; (E) Silica in February; (F) Silica in August.

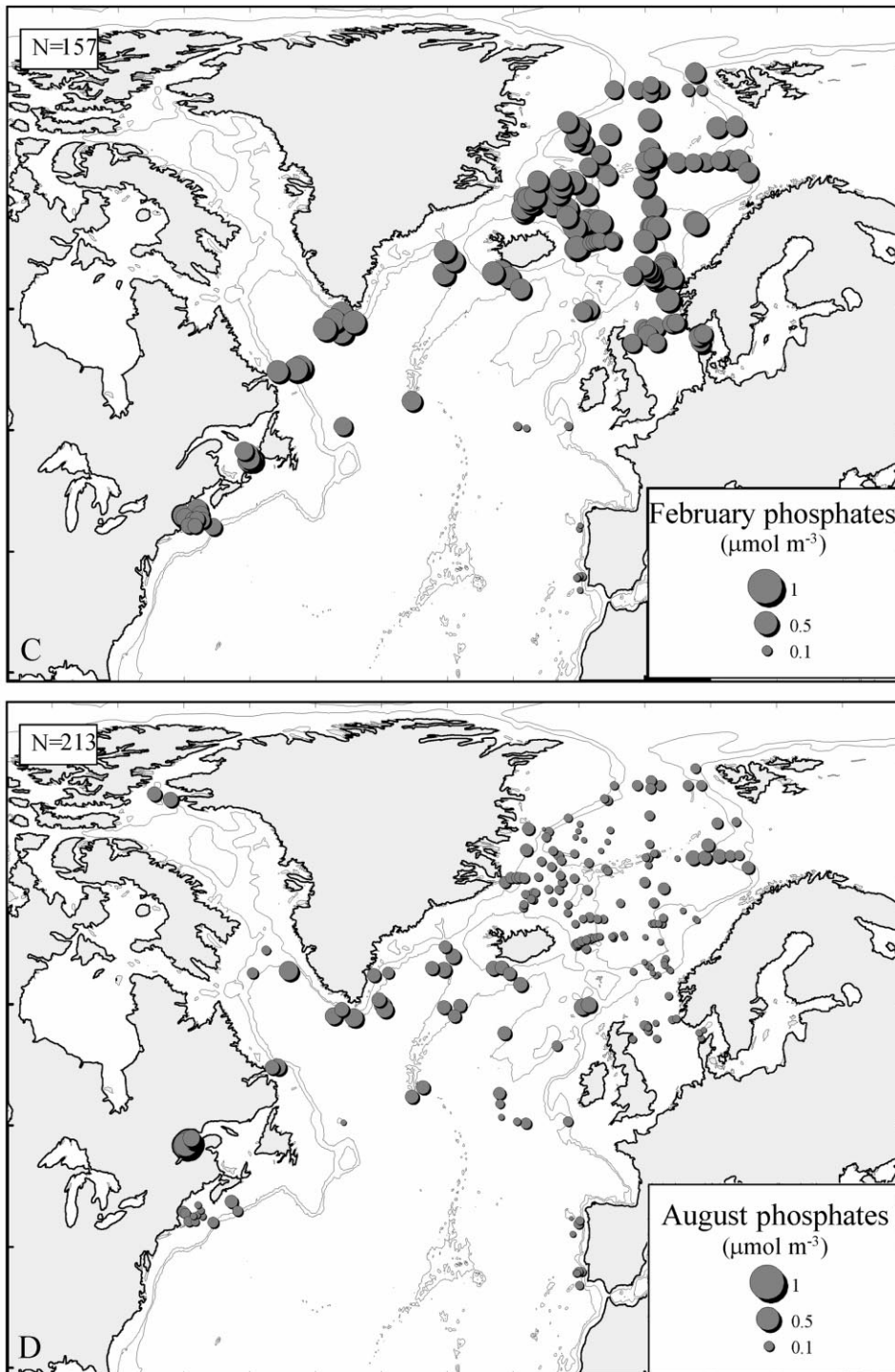


Fig. 4. (continued)

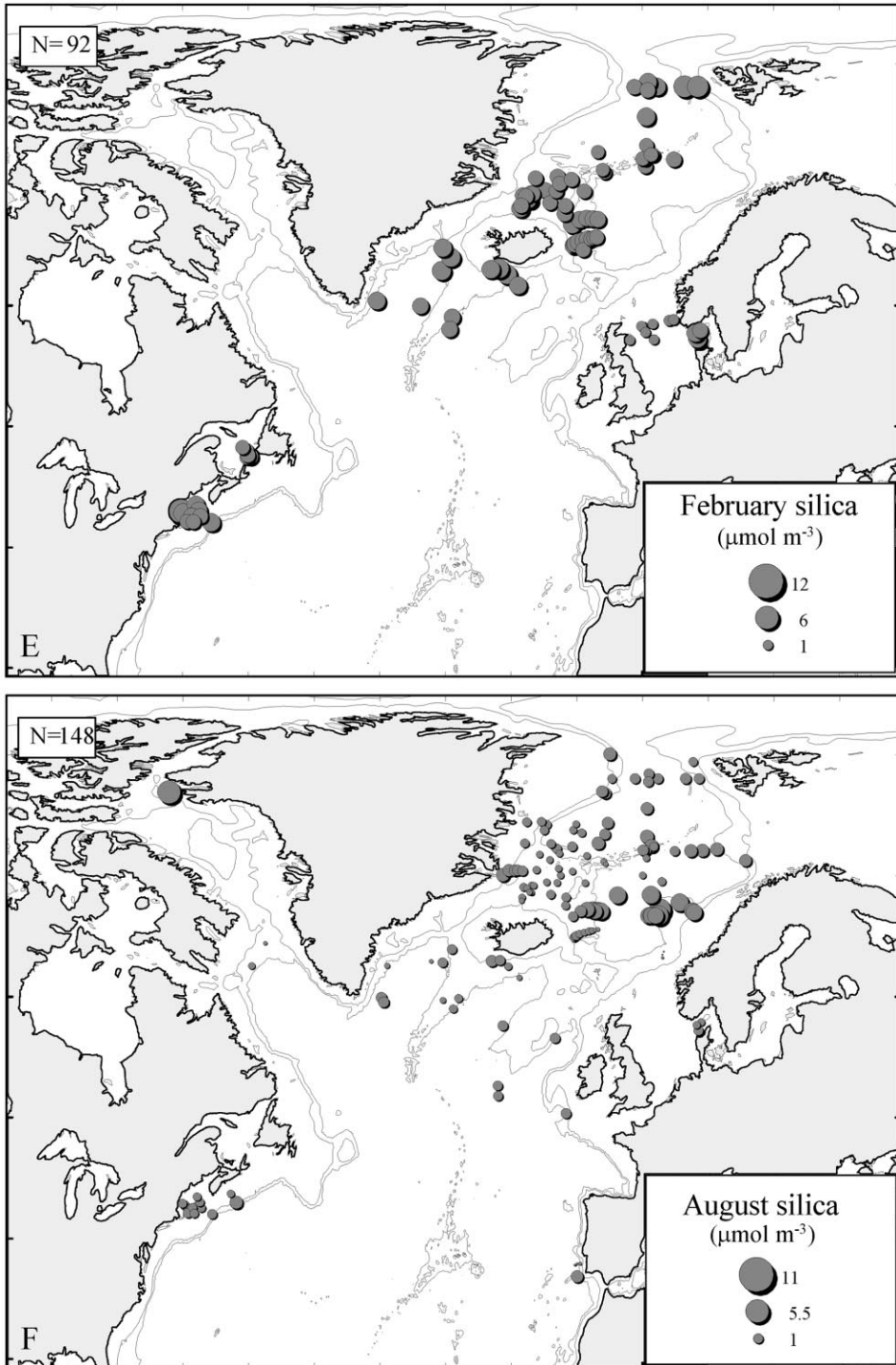


Fig. 4. (continued)

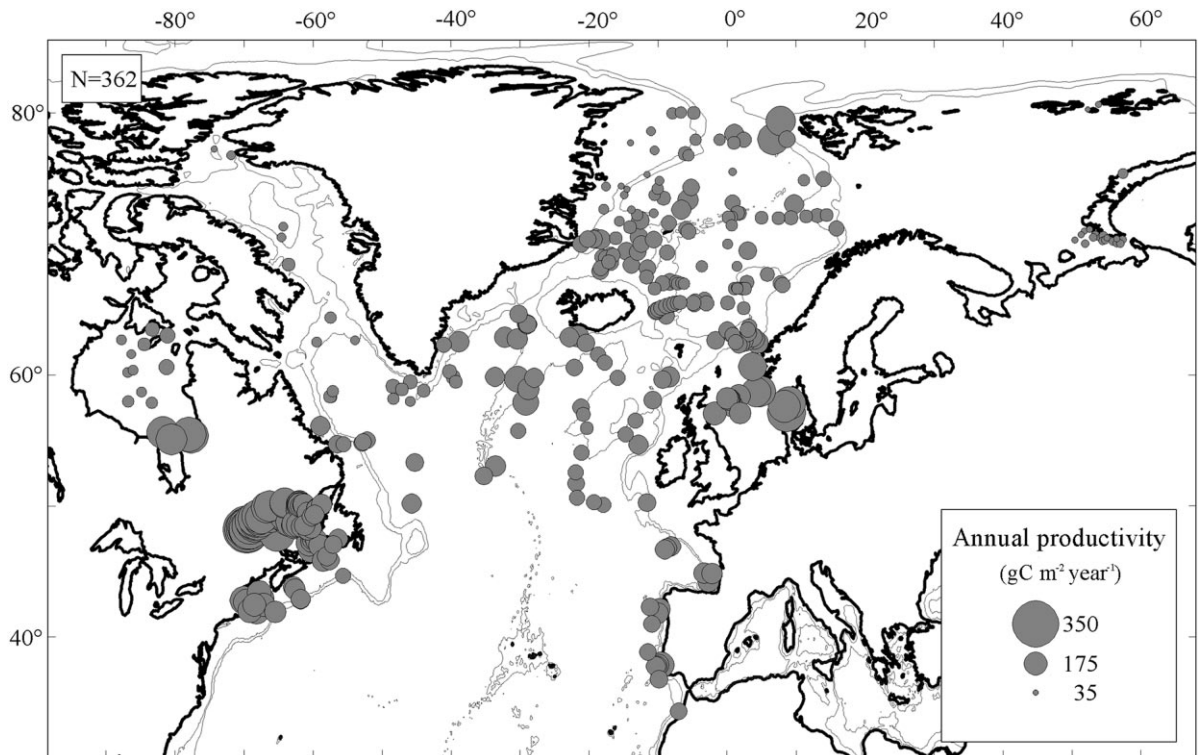


Fig. 5. Distribution of the mean annual primary productivity ($\text{gC m}^{-2} \text{year}^{-1}$) in the euphotic layer. The data are derived from chlorophyll-like pigment measurements through remote sensing (cf. Antoine and Morel, 1996).

(after logarithmic transformation) and the principal components using the D-27 and D-20 data sets, the concentrations of nutrients and the annual productivity. Coefficients of correlations with $p \leq 0.05$ were considered to be significant. Calculations were made using the SAS software (1990).

In addition to currently used statistical treatments, we tested two types of transfer functions with different statistical procedures in order to evaluate the respective accuracy of the methods for the reconstruction of productivity and nutrients.

- (i) The first type relies on multiple regressions, as developed by Imbrie and Kipp (1971). Both the D-20 and D-27 dinocyst data sets were used to estimate nitrates, phosphates and silica concentrations in February and August and the monthly, seasonal and annual productivity. The maximum R regression method was performed on the basis of the SAS software (1990). This method include

variables in the model according to a decreasing order of the correlation coefficients (R) between dinocyst taxa and the environmental parameter to reconstruct.

- (ii) The second type of approach relies on the best analogue technique. It was used to tentatively reconstruct nitrates and phosphates in February as well as the annual productivity on the basis of both D-20 and D-27 data sets. The software is from Guiot (1990) and the protocol is basically the same as that described for the reconstruction of hydrographical parameters (cf. de Vernal et al., 1997; Rochon et al., 1999). It consists of a logarithmic transformation of taxa percentages and a search of analogues in the modern database with even weight for all taxa. A set of five analogues was considered for nutrients because of the limited number of data, whereas 10 analogues were searched to estimate productivity. For validation, the search for analogues is made after

exclusion of the spectrum to analyze. The best estimate is calculated on the basis of the weighted average of the values corresponding to the analogues selected in the reference database. Taxa are weighted evenly in this analysis.

The reliability of the methods is evaluated on the basis of the linear regression between observations and reconstructions. The residuals, i.e. the differences between instrumental and reconstructed values, allowed us to define the degree of accuracy of the reconstructions.

3. Dinocyst assemblages and nutrients

3.1. Dinocyst distribution

In the D-27 data set, the first two principal components (PC) represent respectively 57 and 16% of the variance, whereas the other components explain less than 10%. Thus, only PC1 and PC2 were considered for statistical analysis. The geographical distributions of PC1 and PC2 are shown in Fig. 6a and b. The PC1 shows a gradient from the northwestern North Atlantic, having negative values, to the southeastern part of our dinocyst data set, having higher values (Fig. 6a). The highest values are observed on the western side of the French and Iberian margins. The geographical distribution of the PC2 shows the highest values on the eastern side of Greenland, the western side of the Gibraltar Strait and close to the Quebec margins (Fig. 6b). The weighting of taxa (Fig. 3) according to PC1 shows an opposition between the temperate Gonyaulacale taxa (*Spiniferites* spp. and *Impagidinium* spp.) and the cold water taxa (*Algasphaeridium? minutum*, *Pentapharsodinium dalei* and *Impagidinium pallidum*). There is a strong correlation between PC1 and hydrographic parameters, notably the temperatures in February and August, that illustrate the determinant control of thermal conditions (Fig. 7a). Relationships are weaker between PC2 and the environmental parameters selected for this study. Nevertheless, a positive relationship links PC2 and the percentages of heterotrophic taxa, with a correlation coefficient of 0.83 (Fig. 7b). This illustrates that the trophic behavior is also a determinant parameter in the distribution of assemblages.

In the D-20 data set, PC1 and PC2 represent, respectively, 64 and 13% of the variance. As in the D-27 data set, PC1 is principally explained by hydrographic variables, in particular the February sea-surface temperature ($R = 0.70$). PC2 shows some correlation with the August sea-surface temperature ($R = 0.59$) (Fig. 7a).

3.2. Nutrient distribution

Nitrate, phosphate and silica concentrations are much lower in August than in February (Fig. 4), as a result of biological uptake during spring and summer (e.g. Parsons et al., 1984; Summerhayes and Thorpe, 1996). The nutrient concentrations in February can therefore be associated with their availability in surface waters, prior to the blooming seasons.

Nitrate concentrations range from 1.36 to 15.84 $\mu\text{mol m}^{-3}$ in February, and from 0.18 to 7.32 $\mu\text{mol m}^{-3}$ in August (Fig. 4a and b), whereas phosphate concentrations range from 0.07 to 1.05 $\mu\text{mol m}^{-3}$ in February, and from 0 (not detectable) to 0.97 $\mu\text{mol m}^{-3}$ in August (Fig. 4c and d). Nitrate and phosphate concentrations correlate as is generally the case in oceanic water (Redfield et al., 1963). The coefficients of correlation (R) between nitrates and phosphates are 0.79 and 0.74 for February and August respectively (Table 1). The slopes defined by the linear regressions are 10.5 in February and 7.5 in August. These slopes are much lower than the N:P Redfield ratio of 15:1 (Redfield et al., 1963). However, the February N:P ratio of 7.5 is very close to the N:P ratio of 6.2 that is recorded in February on the scale of the North Atlantic (data compiled after the NODC data set, 1994; see also Tyrell and Law, 1997). The generally low N:P ratio and its decrease in August suggests that nitrate is a limiting factor for North Atlantic primary productivity (cf. Karl et al., 1997). The higher N:P ratio in February is probably related to vertical mixing in winter (Brown et al., 1989).

Dissolve silica concentrations range from 2.53 to 11.54 $\mu\text{mol m}^{-3}$ in February, and from 0 to 10.05 $\mu\text{mol m}^{-3}$ in August (Fig. 4e and f). Silica concentrations are higher in February because of water mixing (Brown et al., 1989) in addition to lower solubility in cold water. Silica concentrations

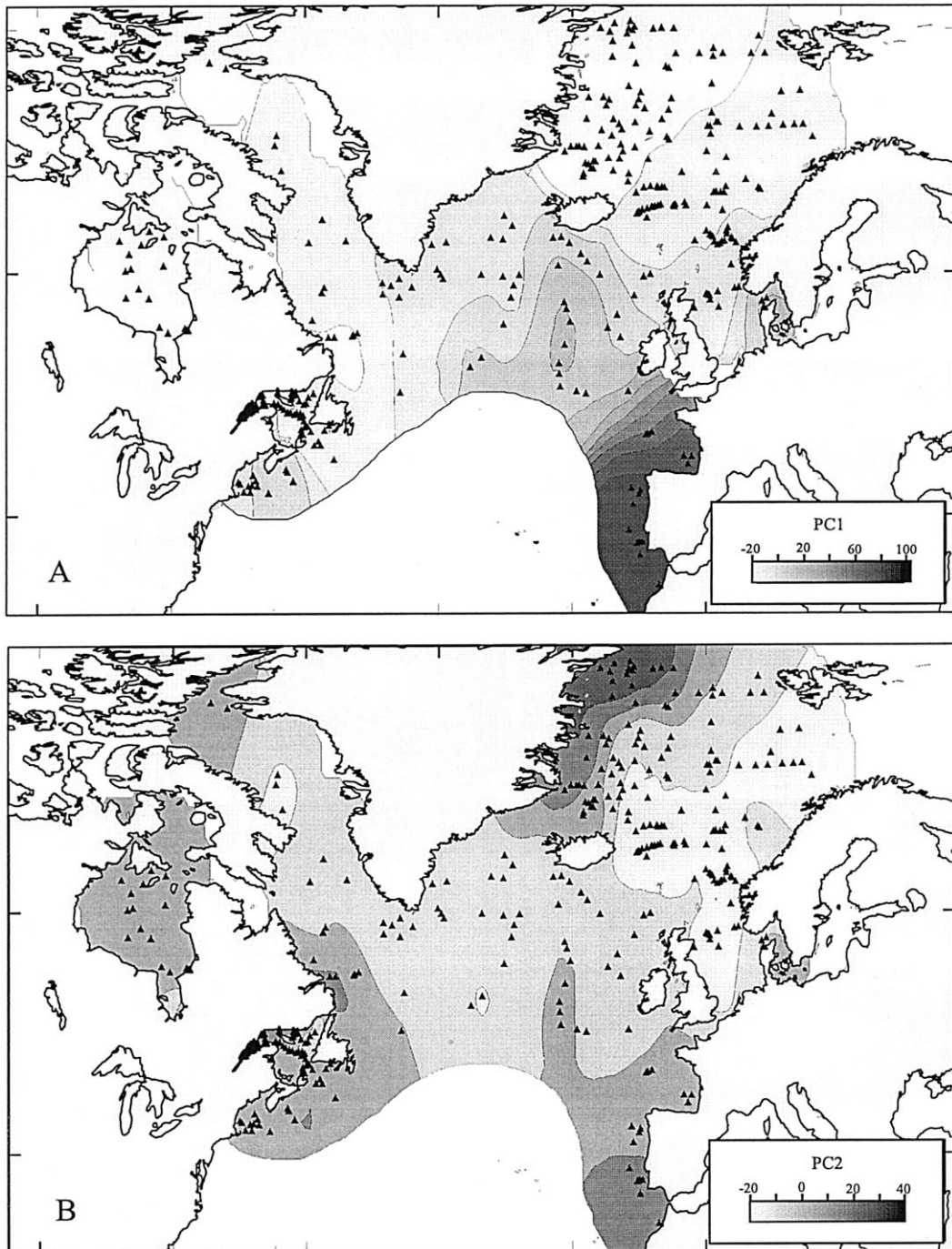


Fig. 6. (A) Distribution of the first principal component (PC1) for the D-27 data set. PC1 represents 57% of the variance. Interpolation is made with an Inverse Distance Weighting (IDW) algorithm using the Vertical Mapper software. (B) Distribution of the second principal component (PC2) for the D-27 data set. PC2 represents 16% of the variance.

are also much lower in August because of diatom consumption.

Correlation coefficients between nutrients, temperature and salinity were also calculated in order to verify the interdependency of these variables (Table 1). The regression depicts inverse relationships between the nitrate concentration and the temperature in February ($R = 0.56$), and between the phosphates and the salinity in August ($R = 0.62$). An interdependency of these parameters on the scale of the North Atlantic would need consideration.

3.3. Relationships between dinocysts and nutrients

The links between nutrient concentrations and the percentage of dinocyst taxa in the assemblages were explored with Pearson's correlation (Table 2). Most correlation coefficients are lower than 0.50, with a few exceptions. Nitrate and phosphate concentrations in February are the variables that show the most significant relationship with a few taxa. *Nematosphaeropsis labyrinthus* is positively correlated with nitrates in February ($R = 0.72$), whereas *Impagidinium aculeatum* ($R = 0.50$), *Impagidinium patulum* ($R = 0.60$), *Spiniferites ramosus* ($R = 0.55$), *Spiniferites mirabilis* ($R = 0.57$) and *Lingulodinium machaerophorum* ($R = 0.63$) are negatively correlated according to linear regressions. Similar links are observed using either the D-20 data set, or the D-27 data set (Table 2). With the exception of *Impagidinium sphaericum*, species of the genus *Impagidinium* show an oligotrophic behavior.

Statistical analyses also reveal a significant correlation between PC1 and nitrate and phosphate concentrations in February, with coefficients of correlation slightly higher when considering the autotrophic taxa exclusively (cf. Table 2). PC2 is apparently not related to the distribution of nutrients in the D-20 data set, but shows some relationships with nitrates in February in the D-27 data set, i.e. when heterotrophic taxa are included (Fig. 8).

4. Dinocysts and productivity

4.1. Productivity distribution

In the database, the annual productivity ranges from 42 to 359 gC m⁻² yr⁻¹ (Fig. 5). This data set is

representative of global ocean productivity considering that more than 99.5% of the global productivity data range between 0 and 400 gC m⁻² year⁻¹. However the data set precludes upwelling regions, with the exception of the seasonal upwelling situated along the Portugal margins. Areas having a high primary productivity are principally located along continental margins, such as the Gulf and Estuary of the St. Lawrence, the North Sea and the southern Hudson Bay. Relatively low productivity areas are located in the cold areas of Baffin Bay and the eastern Barents Sea.

There are tenuous links between annual productivity and nutrients. However, inverse relationships are observed between productivity and salinity in February ($R = 0.54$) and August ($R = 0.56$) (Table 1). This can be explained by a higher productivity in coastal and neritic water when river discharges are responsible for both dilution and nutrient input in surface waters.

4.2. Relationships between dinocysts taxa and the annual productivity

The correlation matrix of Table 2 reveals that there are no obvious links between annual productivity and dinocyst taxa percentages, either with the D-20 data set, or with the D-27 data set. The only taxon showing some correlation with annual productivity ($R > 0.5$) is *Selenopemphix quanta*, that is related to an heterotrophic dinoflagellate (Table 2). There is no correlation between productivity and PC1. However, there is a significant relationship between productivity and PC2, especially when using exclusively the autotrophic taxa ($R = 0.45$).

5. Validation of transfer functions for nutrient and productivity database

Transfer functions using multiple regression techniques were tested with both D-27 and D-20 data sets for tentative reconstruction of nutrient and productivity (Table 3). The best analogue technique was also tested for the reconstruction of nitrates and productivity. Among nutrients, nitrates in February is the variable that is best reconstructed, with coefficients of correlation of $R = 0.92$ and $R = 0.89$ between observed and estimated values with the multiple

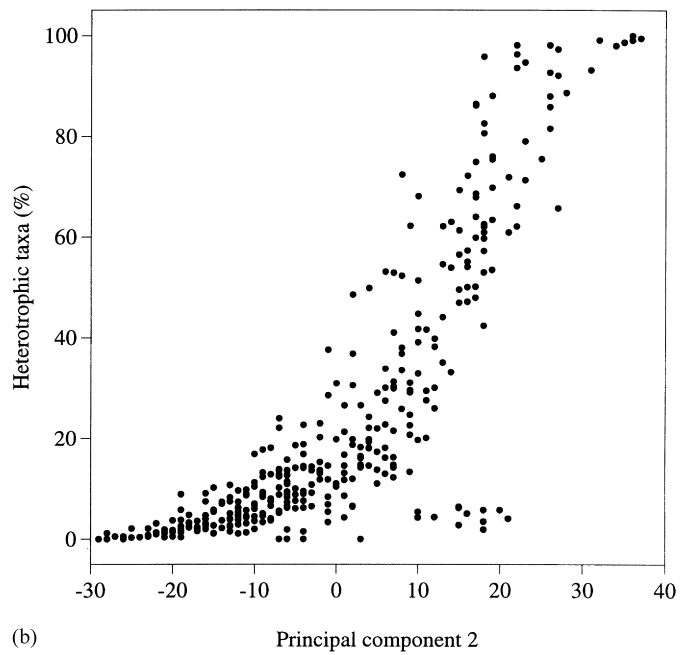
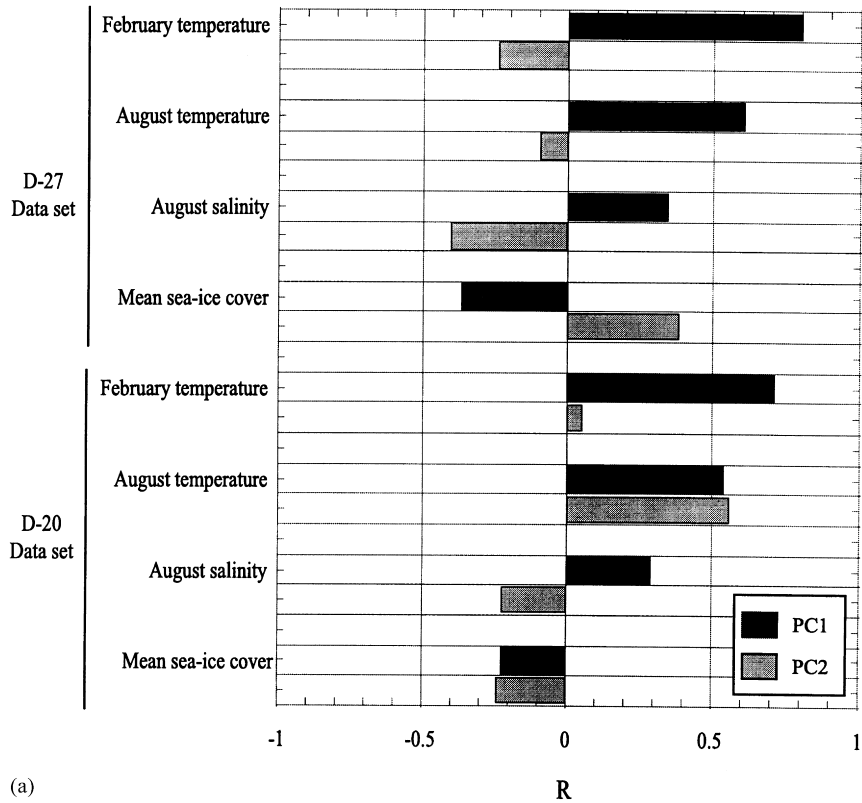


Fig. 7.

Table 1

Nutrient, productivity and hydrological parameters correlation matrix. Only significant coefficients of correlation ($p \leq 0.05$) are reported

	February nitrates	August nitrates	February phosphates	August phosphates	February silica	August silica	Annual productivity	February temperature	August temperature	August salinity
February nitrates	×	0.42	0.79	0.47	–	–	0.52	– 0.56	– 0.76	–
August nitrates	0.42	×	–	0.74	–	–	0.39	–	–	– 0.38
February phosphates	0.79	–	×	–	–	0.24	0.23	– 0.45	– 0.42	–
August phosphates	0.47	0.74	–	×	0.50	–	0.50	– 0.19	–	– 0.62
February silica	–	–	–	0.50	×	–	–	–	–	–
August silica	–	–	0.24	–	–	×	0.26	– 0.59	–	–
Annual productivity	0.52	0.39	0.23	0.50	–	– 0.26	×	–	0.46	– 0.56
February temperature	– 0.56	–	– 0.45	– 0.19	–	0.59	–	×	0.58	0.59
August temperature	– 0.76	–	– 0.42	–	–	–	0.46	0.58	×	–
August salinity	–	– 0.38	–	– 0.62	–	–	– 0.56	0.59	–	×

Coefficients with $R > 0.5$ are indicated in bold.

regression method and the best analogue method respectively (Fig. 9). The residuals indicate that this method allows a reconstruction of February nitrates with an accuracy of 1.25 or 1.42 $\mu\text{mol m}^{-3}$ (Table 3). Taking into account the inherent limits of the nutrient and the dinocyst databases, such results appear reliable. The tentative reconstruction of phosphates and silicates led to calculation of coefficients of correlation between estimated and observed values that are lower than 0.80, therefore precluding reconstruction based on dinocysts.

Reconstructions of productivity with the best analogue technique yield reasonable results with a correlation coefficient between observations and estimates of $R = 0.89$ (cf. Fig. 9b). The residuals indicate an accuracy of 26.5 $\text{gC m}^{-2} \text{yr}^{-1}$ (Table 3). Such accuracy is of the same order as the uncertainty of productivity estimations from remote sensing. Similar results, although slightly weaker, are obtained with use the D-20 data set instead of the D-27 data set (cf. Table 3).

6. Discussion and conclusions

The establishment of relationships between two

sets of parameters, the dinocyst distribution and the nutrient data, is difficult. There are limitations due to the paucity of nutrient data that prevented the establishment of a uniform data set with respect to the sample site location for all the parameters measured. Moreover, there are sources of error with respect to the accuracy and temporal dimension of both the dinocyst and nutrient data sets. Despite these difficulties, we have documented some of the relationships between dinocyst assemblages and the nutrient concentrations and primary productivity of the upper water column throughout the North Atlantic.

In addition to the direct influence of the temperature, salinity and sea–ice cover (cf. de Vernal et al., 1997; Rochon et al., 1999), the distribution of the dinocyst taxa also seems to be controlled by the trophic behavior of the original dinoflagellate population. The structure of the cyst populations, with respect to autotrophic vs. heterotrophic affinities of their thecate stage, explains part of the distribution of the assemblage as observed herein. There is also a relationship between the concentration of nutrients and the dinocyst distribution. In particular, the concentration of nitrates and phosphates in February correlates with the assemblages as defined from multivariate analyses. The closest relationship is observed

Fig. 7. (A) Coefficients of correlation between the principal components 1 and 2, and the temperature, salinity and sea–ice cover using the D-27 and the D-20 data sets. The coefficients of correlation are calculated after linear regression. The coefficients are slightly higher when using polynomial relation. (B) Sum of the heterotrophic taxa percentages (Fig. 2b) vs. the principal component 2 for the D-27 data set. The coefficient of correlation is $R = 0.83$, according to linear regression. The few data points out of the distribution (gray zone) correspond to sites located on the west side of Portuguese and French coasts.

Table 2

Matrix of correlation coefficients between the dinocyst taxa percentages, principal components 1 and 2, and the nutrient and productivity data. Heterotrophic taxa are indicated by an asterisk. The dinocyst percentages were transformed in logarithmic values. The coefficients of correlation are calculated on the basis of linear regressions. Only significant coefficients of correlation ($p \leq 0.05$) are reported and coefficients with $R > 0.5$ are indicated in bold characters. In general, weaker coefficients of correlation were obtained by using arithmetic values of percentages

	D-27 data set							D-20 data set						
	February nitrates	August nitrates	February phosphates	August phosphates	February silica	August silica	Annual productivity	February nitrates	August nitrates	February phosphates	August phosphates	February silica	August silica	Annual productivity
<i>Operculodinium centrocarpum</i>	–	–0.16	–	–0.42	–	0.23	–0.25	–	–	–	–0.26	–	0.33	–0.22
<i>Nematosphaeropsis labyrinthus</i>	0.72	–	0.49	–	–	–	–0.14	0.72	–	0.50	–	–	–	–0.12
<i>Pentapharsodinium dalei</i>	–	–	0.36	–	–	–	0.25	–	–	0.37	0.23	–	–	0.32
* <i>Trinovantedinium applanatum</i>	0.22	0.27	–	–	0.25	–	–	–	–	–	–	–	–	–
* <i>Algidasphaeridium ? minutum</i>	–	–	–	0.29	–	–	0.15	–	–	–	–	–	–	–
* <i>Brigantedinium</i> spp.	–	0.30	–	0.42	0.25	–	0.27	–	–	–	–	–	–	–
*Congruentidiacean	–0.34	–	–0.28	–	–	–	–	–	–	–	–	–	–	–
* <i>Polykrikos schwartzii</i>	0.24	0.24	0.17	–	–	–	–	–	–	–	–	–	–	–
* <i>Selenopemphix quanta</i>	–	0.43	0.22	0.48	–	–	0.57	–	–	–	–	–	–	–
<i>Alexandrium tamarense</i>	–0.42	–	–	–	–	–	0.14	–0.43	–	–	–	–	–	0.14
<i>Bitectatodinium tepikiense</i>	–0.25	–	–	–0.19	–0.40	–	0.17	–0.26	–	–	–0.15	–0.37	–	0.19
<i>Impagidinium aculeatum</i>	–0.50	–	–0.53	–	–	–	–	–0.50	–	–0.53	–	–	–	–
<i>Impagidinium patulum</i>	–0.60	–0.18	–0.47	–	–	–	–	–0.61	–0.19	–0.47	–	–	–	–
<i>Impagidinium paradoxum</i>	–0.44	–	–0.49	–	–	–	–	–0.39	–	–0.47	–	–	–	–
<i>Impagidinium sphaericum</i>	0.36	0.31	–	0.15	0.26	–	–0.12	–	0.21	–	–	0.33	–	–
<i>Impagidinium striolatum</i>	–0.47	–	–0.48	–	–	–	–	–0.47	–	–0.48	–	–	–	–
<i>Spiniferites</i> spp.	–0.63	–	–0.52	–0.20	–	–	0.20	–0.63	–	–0.50	–	–	–	0.21
<i>Spiniferites bentorii</i>	–0.35	–	–0.37	–	0.21	–	–	–0.36	–	–0.38	–	0.21	–	–
<i>Spiniferites ramosus</i>	–0.55	–	–0.19	–	–0.27	–0.21	0.38	–0.56	–	–0.17	–	–0.25	–0.20	0.42
<i>Spiniferites elongatus</i>	–	0.13	–	0.15	0.39	–	–0.13	–	0.18	–	0.31	0.41	–	–
<i>Spiniferites membranaceus</i>	–0.47	–	–0.52	–	–	–	–	–0.47	–	–0.52	–	–	–0.16	–
<i>Spiniferites mirabilis</i>	–0.57	–0.20	–0.57	–0.05	–	–	–	–0.58	–0.20	–0.57	–0.17	–	–	–
<i>Lingulodinium machaerophorum</i>	–0.63	–	–0.59	–	–	0.17	–	–0.64	–	–0.59	–	–	–0.17	–
<i>Pyxididopsis reticulata</i>	–0.44	–	–0.39	–	–	–0.19	–	–0.44	–	–0.39	–	–	–0.19	–
<i>Ataxodinium choane</i>	–	–	–	–	–	–	0.26	–	–	–	–	–	–	0.28
<i>Impagidinium ? pallidum</i>	0.31	–0.18	–	–0.26	–	–	–0.33	0.31	–0.19	–	–0.23	–	–	–0.36
* <i>A ? minutum</i> var. <i>cezare</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PC1	–0.66	–	–0.62	–0.16	–	–	–	–0.71	–	0.65	–	–	–	–
PC2	–0.53	0.18	–0.33	0.37	0.30	–	0.31	–0.31	–	–	0.26	–	–	0.45

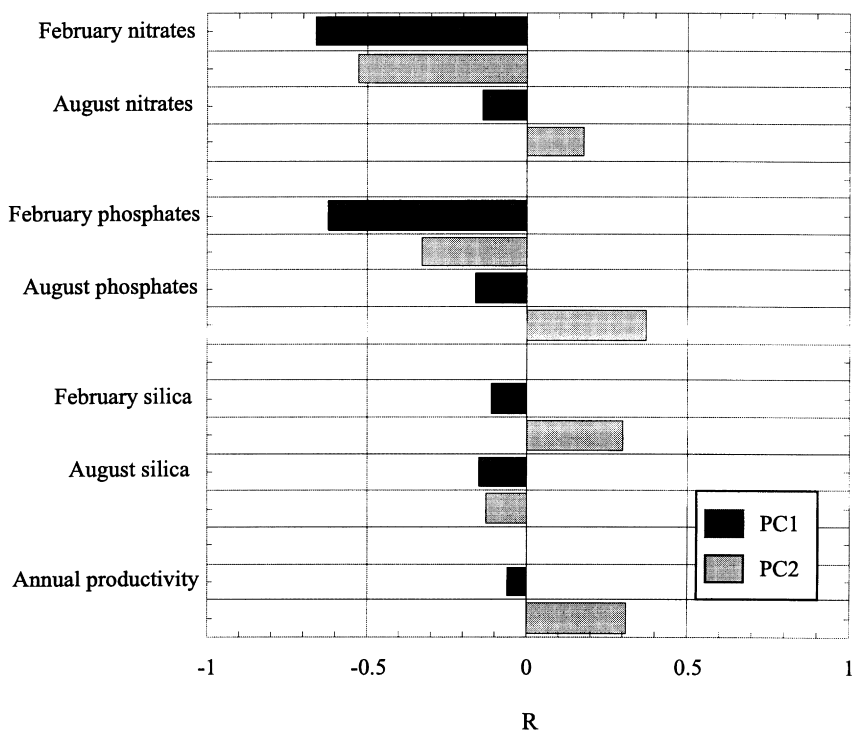


Fig. 8. Coefficients of correlation between the principal components 1 and 2, and the nutrient concentrations and productivity using the D-27 data set. The coefficients of correlation are calculated after linear regression. The coefficients are slightly higher when using polynomial relation.

between the cyst assemblages and the concentration of nitrates in February providing a measurement of nitrate availability in the surface waters prior to the blooming season after the winter. Amongst the dinocyst taxa, *Nematosphaeropsis labyrinthus* appears to have an eutrophic behavior, whereas *Impagidinium aculeatum*, *Impagidinium patulum*, *Lingulodinium machaerophorum*, *Spiniferites mirabilis* and *Spiniferites ramosus* seem to be oligotrophic. The almost exclusive open ocean affinities of *Impagidinium patulum* and *Impagidinium aculeatum* might be linked to the oligotrophic characteristics of their thecal stage.

In addition to relationship with nitrates, there is an apparent link between the cyst distribution and phosphate; this could, however, be fortuitous and be related to the interdependency of nitrates and phosphates (Table 1). There is no observed relationship between the dinocyst taxa, their assemblages and silica. This is not surprising since silica is not the limiting factor for dinoflagellates as it is for diatoms (Sommer, 1989).

It is generally admitted that nitrates constitute a limiting factor for net primary productivity in the oceans and play a determinant role in the development of dinoflagellate populations (e.g. Sevrin-Reyssac, 1983; Parsons et al., 1984; Taylor, 1987). A close relationship between dinoflagellate productivity and nitrogen availability was documented by in vivo or in vitro studies (Spector, 1984; Taylor, 1987). Our study also illustrates the importance of nitrogen on dinoflagellate hypnozygotic cysts that provide a fragmentary picture of the original dinoflagellate populations. In addition to nitrates, various nitrogen compounds such as ammonia could play a role in phytoplankton productivity as shown by Barnes and Hughes (1982) and Planas et al. (1999), for example. Similarly, several studies have demonstrated that iron can enhance the fertilization of ocean and the net productivity (Sunda et al., 1991; Martin et al., 1994). However, it was not possible to evaluate the relationships between these elements and the dinocyst assemblages because of the scarcity of instrumental data for either ammonia or iron.

On the basis of the close link that exists between

Table 3
Coefficients of correlation (R) between observations and reconstructions using different transfer function techniques: multiple regressions and best analogue approach. The residuals (σ), which correspond to the standard deviation of the difference between observations and reconstructions, yield the degree of accuracy of the estimates

	Multiple regressions						Best analogues					
	D-27 Data set			D-20 Data set			D-27 Data set			D-20 Data set		
	N	R	σ	R	σ	R	σ	R	σ	R	σ	
February nitrates	85	0.62	$\pm 3.26 \mu\text{mol m}^{-3}$	0.92	$\pm 1.25 \mu\text{mol m}^{-3}$	0.89	$\pm 1.42 \mu\text{mol m}^{-3}$	0.88	$\pm 1.49 \mu\text{mol m}^{-3}$	0.88	$\pm 1.49 \mu\text{mol m}^{-3}$	
February phosphates	157	0.71	$\pm 0.158 \mu\text{mol m}^{-3}$	0.70	$\pm 0.158 \mu\text{mol m}^{-3}$	0.72	$\pm 0.155 \mu\text{mol m}^{-3}$	0.71	$\pm 0.157 \mu\text{mol m}^{-3}$	0.71	$\pm 0.157 \mu\text{mol m}^{-3}$	
Annual productivity	362	0.71	$\pm 41.6 \text{gC m}^{-2} \text{yr}^{-1}$	0.58	$\pm 47.9 \text{gC m}^{-2} \text{yr}^{-1}$	0.89	$\pm 26.5 \text{gC m}^{-2} \text{yr}^{-1}$	0.81	$\pm 34.5 \text{gC m}^{-2} \text{yr}^{-1}$	0.81	$\pm 34.5 \text{gC m}^{-2} \text{yr}^{-1}$	

dinocyst assemblages and nitrate concentrations, two types of transfer functions were tested. Both approaches permitted the reconstruction of nitrate concentrations in February as demonstrated by validation tests. The multiple regression method yielded a slightly stronger correlation between the observations and estimates ($R = 0.92$), and the residuals indicate an accuracy of $1.25 \mu\text{mol m}^{-3}$. Similar results are obtained with the analogue method yielding a correlation coefficient of 0.89 between the observed and reconstructed values, and the residuals indicate an accuracy of $1.42 \mu\text{mol m}^{-3}$. The low number of data points for nitrates ($N = 85$) limits the use of the analogue approach and the addition of more reference data points is needed to strengthen the reconstructions.

The productivity data, as estimated from remote sensing measurements, allows a continuous spectrum in space, at the scale of the North Atlantic, that is an advantage in our comparisons because of the scarcity of in situ measurements available. Remote sensing also permits monitoring over many years, which yields better averages for regions characterized by high interannual variability. However, the degree of accuracy of the instrumental estimates is about 17% (Antoine and Morel, 1996) and the uncertainties are even larger in coastal environments marked by highly turbid surface water. In the northern North Atlantic dinocyst data set, there are only weak relationships between the relative percentages of individual taxa and the annual productivity as measured by remote sensing. *Selenopemphix quanta*, which is the cyst of an heterotrophic taxon, is the only one to show a relationship with productivity. Dale and Fjellså (1994) also suggested that this taxon is a high productivity indicator. Multivariate analyses indicate some links between the dinocyst assemblages and productivity, mostly when heterotrophic taxa are excluded from the analyses. The best analogue technique provides reliable estimations with an accuracy of $26.5 \text{gC m}^{-2} \text{year}^{-1}$, that falls within the range of uncertainties of the remote sensing method used for primary productivity estimates. However, multiple regression techniques failed to provide reliable reconstruction, probably because of the non-linear relation between distribution of dinocysts and productivity.

On the basis of our analyses, reconstructions of

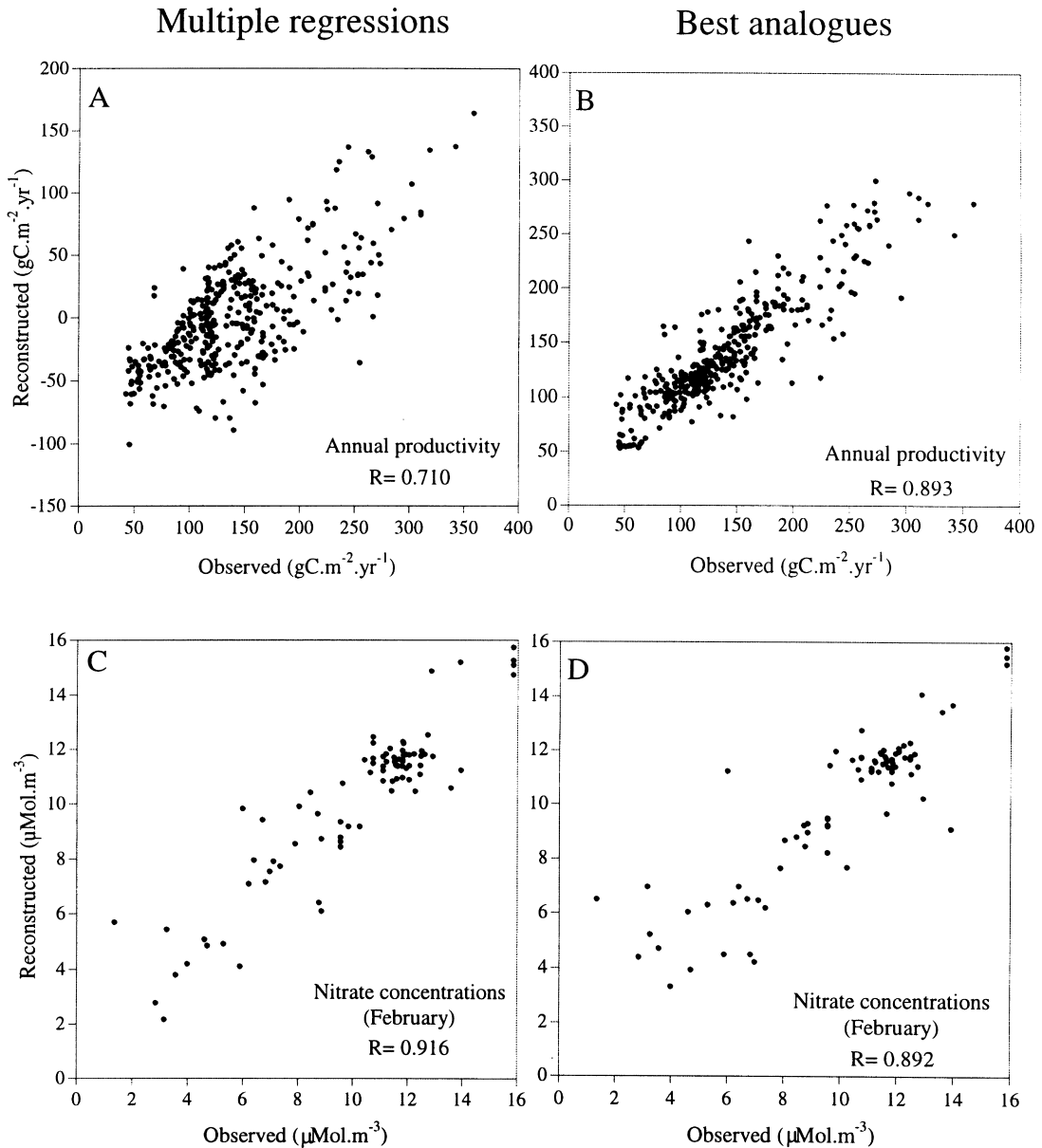


Fig. 9. Relations between observed and reconstructed values for the annual productivity (A and B) and for nitrate concentrations in February (C and D) using a multiple regression technique (A and C) and a best analogue technique (B and D).

paleoproductivity and paleo-nitrate would be possible using dinocyst assemblages. Such an approach should be improved by a larger data set. Regional studies in a same climatic zone, regarding to temperature and salinity, would permit to better constrain the influ-

ence of the interdependency between environmental variables on the observed relations. It will also permit to develop more confidently transfer functions for the reconstruction of paleo-productivity and paleo-nitrates.

Acknowledgements

This work was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche du Québec (FCAR). Thanks are due to D. Antoine who kindly provided productivity data. We are grateful to D. Planas (UQAM), J. Guiot (IMEP, U. de St. Jérôme) and Odile Peyron (GEOTOP, UQAM) for their critical review of the manuscript. The constructive comments of journal reviewers, Rex Harland and an anonymous reviewer helped to prepare the final version of the manuscript.

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