

Hydroclimatic modulation of diatom/*Phaeocystis* blooms in nutrient-enriched Belgian coastal waters (North Sea)

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Abstract

Statistical analysis of 14 yr (1988–2001) of intensive phytoplankton monitoring at Station 330 in the central Belgian Coastal Zone (BCZ, Southern Bight of the North Sea) indicates that the long-term diatom biomass trend and the spring dominance of *Phaeocystis* colonies over diatoms are determined by the combined effect of the North Atlantic Oscillation (NAO) and freshwater and continental nitrate carried by the Scheldt. The strong correlation between diatoms and the NAO index is largely explained by the modulating effect of the latter on the water budget at the monitoring station. The relationship between *Phaeocystis* spring blooms and winter NAO (NAO_w) is indirect, better expressed by springtime *Phaeocystis* dominance over diatoms because of the higher response of the latter to the NAO. The spring *Phaeocystis* : diatom bloom ratio is negatively (or positively) linked to positive (or negative) NAO_w values. A complex cascade of events links large-scale NAO index variations with those local meteorological conditions (wind strength and direction, rainfall) that drive the hydrography and water budget of the BCZ. Local meteorological conditions in turn modulate the geographical spread of Scheldt nutrient loads in the coastal zone and ultimately regulate the magnitude of *Phaeocystis* spring blooms by determining winter nitrate enrichment. Hence, the absence of a linear relationship between *Phaeocystis* spring blooms and NAO_w is explained by the nonlinear response of river-based nitrate pulses to NAO due to local wind-driven hydrodynamical forcing.

Large-scale atmospheric variability has a substantial effect on phytoplankton bloom dynamics and species

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Acknowledgments

We are indebted to the captains and crew of the RV *Belgica* and our colleagues from Belgian marine institutions for helping us with sampling at station 330. We also thank Morten D. Skogen for kindly providing the waterflows calculated by the Norwegian Ecological Model System NORWECOM. We thank Elvire Antajan for the spring 2001 diatom and *Phaeocystis* data and Philippe Grosjean for his helpful comments on statistical analysis. Funding for station 330 time series was provided by several Belgian and EU–Environment Programmes since 1988. The present work is a contribution of the Advanced Modelling and Research on Eutrophication (AMORE) and Identification of Zones affected by Eutrophication (IZEUT) projects of the Belgian Programme “Scientific Support Plan for a Sustainable Development Policy—Sustainable Management of the North Sea,” funded by the Belgian Science Policy under contracts MN/DD/20, EV/11/19, and MN/11/93. It is also a contribution to Stream 3 (Nutrient-driven thresholds of environmental sustainability) of the Integrated Project THRESHOLDS (Thresholds of Environmental Sustainability), funded by the European Commission (Global Change and Ecosystems) under contract 003933. Véronique Choquette helped with English improvement, and three anonymous reviewers provided constructive comments on the manuscript.

dominance (Cloern 1996; Yin et al. 1999; Drinkwater et al. 2003), especially in the northwest European shelf seas (Belgrano et al. 1999; Irigoien et al. 2000; Edwards et al. 2001) influenced by the North Atlantic Oscillation (NAO; Hurrell 1995). In the nearshore waters of this area, however, the effect of this large-scale phenomenon interacts with the local influence of river nutrient loads. There has been a considerable increase of freshwater nitrogen (N) and phosphorus (P) inputs to these coastal waters during the last century as a result of increasing human population density in the watershed and anthropogenic emissions (e.g., Howarth et al. 1996). Over the same period, phytoplankton biomass has increased in many coastal waters, and there has been a shift in species dominance toward nonsiliceous species, apparently as a result of the increase in N and P (e.g., Richardson 1997). In the Southern Bight of the North Sea, recurrent blooms of *Phaeocystis* colonies (*Phaeocystis globosa*; Rousseau, unpubl. data) occur after a bloom of diatoms in early spring. Whereas the diatom bloom is controlled by silicates and phosphates (Rousseau 2000), *Phaeocystis* blooms are sustained by nitrate excess (Lancelot et al. 1998). Attempts have been made to relate long-term fluctuations of these blooms to basin-scale processes driven by climate change (Owens et al. 1989) or to the local influence of freshwater N and P inputs (e.g., Cadée and Hegeman 1991), but the combined effect of these two factors has never been investigated. Knowledge of the respective role of climate and river nutrient loads in

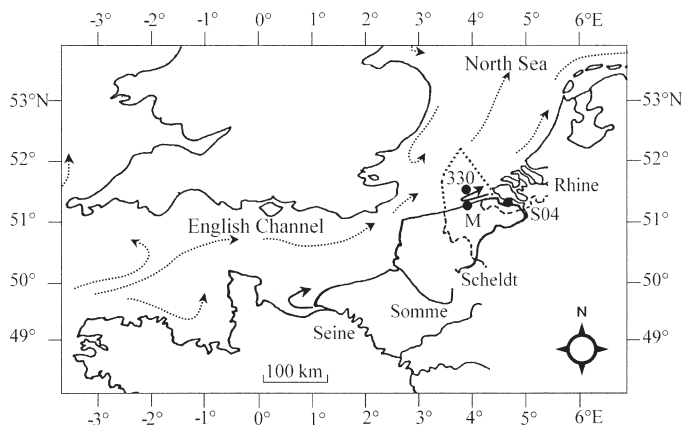


Fig. 1. Map showing the general circulation of water masses (dashed arrows) in the English Channel and the Southern Bight of the North Sea and the main river inputs (black arrows). The dotted line shows the limit of BCZ. Black dots indicate the position of Sta. 330, S04, and Middelkerke (M).

structuring phytoplankton communities is critical to the long-term sustainability of these coastal marine ecosystems.

The Belgian Coastal Zone (BCZ), located in the Southern Bight of the North Sea (Fig. 1), is a relevant site to investigate links between phytoplankton blooms and hydroclimatic and continental forcings. This area is highly dynamic, with water masses resulting from the variable mixing of English Channel Water Inflow (ECWI) coming from the Atlantic and freshwater input from the Scheldt River (Fig. 1). The geographical extent of the river plume is mainly determined by wind direction and speed (Lacroix et al. 2004). Overall nutrient enrichment of the BCZ mainly results from Scheldt inputs, but it results also from the enrichment of ECWI by discharges from the Seine River (Fig. 1).

Between 1988 and 2001, a survey of diatom and *Phaeocystis* blooms at Station 330, in the central BCZ (Fig. 1), was conducted at time intervals ranging from twice a month to twice a week. Diatoms were recorded year-round, while *Phaeocystis* colonies occurred as a spring event lasting between 4 and 13 weeks (Fig. 2). The diatom–*Phaeocystis* succession was observed every year, but the magnitude of the blooms showed important interannual fluctuations, with most years clearly dominated by *Phaeocystis* but a few by diatoms (Fig. 2). Over this period, P loads by the Scheldt River were reduced by about 77% with respect to this level in the early 1980s, but N loads remained unchanged (Rousseau et al. 2004). Yet the phytoplankton time series collected at Sta. 330 did not reveal any corresponding trend in diatom–*Phaeocystis* blooms (Fig. 2; Rousseau 2000). The lack of an observable trend may result from the additional influence of NAO-driven hydroclimatic factors.

In order to investigate the effect of climate variability (NAO index) and human activities (Scheldt nutrient loads) on the magnitude of diatom and *Phaeocystis* blooms in the BCZ, we conducted a serial statistical analysis based on a comprehensive suite of nutrient loads, hydrometeorology, and phytoplankton collected at Sta. 330 between 1988 and 2001.

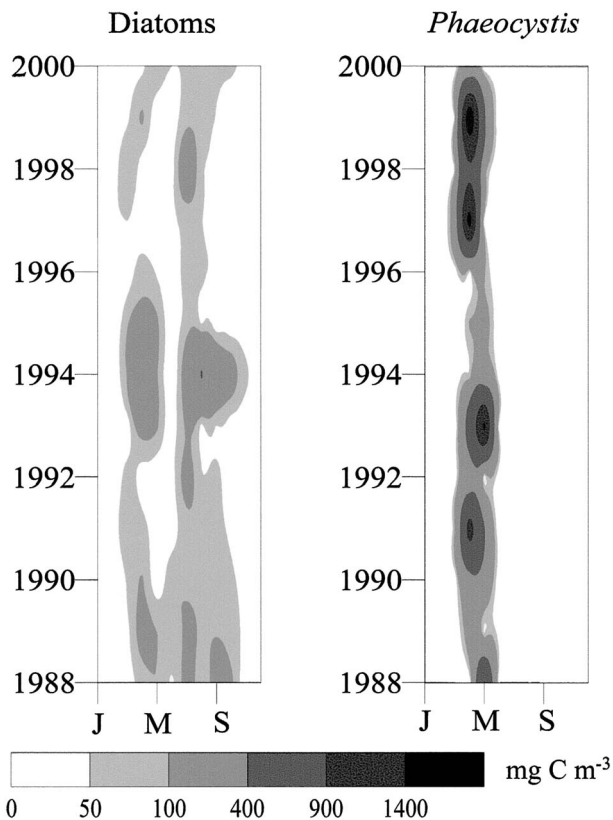


Fig. 2. Seasonal pattern of diatom and *Phaeocystis* colony biomass (mg C m⁻³) at Sta. 330 from 1988 to 2000 (JMS: January, May, September).

Methods

Data sets—Sta. 330: Subsurface seawater was collected throughout the year at Sta. 330 (51°26.05'N, 2°48.50'E; Fig. 1) at weekly intervals, except during winter and summer, when the interval was 2 weeks. From 1988 to 1991 and in 2001, the survey period only ran from February to mid-June. Salinity was measured at a depth of 3 m with a Seacat thermosalinograph (SBE21).

Some 10–50 mL of each sample was preserved for phytoplankton analysis using a 1% (final concentration) Lugol–glutaraldehyde solution. The analysis was performed under inverted microscopy (Leitz Fluovert) according to the Utermöhl method. Over 400 cells were counted in each sample, resulting in 10% error, with a 95% confidence interval (Lund et al. 1958). Magnification was chosen according to cell or colony size: $\times 40$ or $\times 100$ for *Phaeocystis* colonies and $\times 100$ or $\times 200$ for diatoms. Diatom carbon biomass was calculated on the basis of cell concentration and specific biometry using the size-dependent density relationship recommended by Menden-Deuer and Lessard (2000). The carbon biomass of *Phaeocystis* colonies was estimated by biovolume measurement (Rousseau et al. 1990). Our own phytoplankton time series was complemented with available *Phaeocystis* and diatom cell counts for the 2001 spring bloom (Antajan 2004). *Phaeocystis* biomass in 2001 was estimated using a carbon conversion factor of 89.5 pg C cell⁻¹, which is the average

of the two conversion factors suggested by van Rijssel et al. (1997).

Suspended particulate matter (SPM) content was estimated by weighing the particulate matter collected by filtration on a GF/F (Whatman) filter. Nitrate (including nitrite) concentrations were determined according to the Grasshoff (1983) colorimetric method on filtered seawater samples (0.6 μm , Nucleopore) that had been stored frozen until their analysis.

Hydrodynamics: Monthly ECWI in the BCZ was calculated between 1992 and 2000 using a conventional, vertically integrated, two-dimensional model with a resolution of 5' in longitude and 2.5' in latitude (de Vries et al. 1995). State variables included free surface elevation relative to the mean sea level and the two horizontal components of depth mean current. Equations described the shallow water wave based on mass and momentum conservation. Surface and bottom stresses were computed using a quadratic function of surface wind speed and of the mean bottom current. The model was driven by eight tidal constituents along the open boundaries and by meteorological data (six per hour for wind speed and atmospheric pressure) obtained from the U.K. Meteorological Office. In the absence of in situ data for the period of interest, calculated water flows were compared with those obtained from the three-dimensional NORWECOM model (Skogen et al. 1995). Month-to-month variations of the two model results for the available period (1992–1998) were closely related ($r^2 = 0.86$, $p < 0.001$, $n = 84$).

The amount of freshwater at Sta. 330 was estimated based on salinity difference between Sta. 330 (S_{330}) and Sta. S04 (S_{S04}) in the Scheldt Estuary (51°21'N, 3°49.8'E; Fig. 1), normalized to S_{S04} . S_{S04} data (1992–1997) were downloaded from the ICES website (<http://www.ices.dk/ocean/>). Monthly Scheldt runoff ($\text{m}^3 \text{s}^{-1}$) was obtained from the Department of Environment and Infrastructure (Ministry of Flemish Community, Belgium).

NAO index and meteorological data: Monthly and winter (NAO_w) NAO index data were downloaded from the National Center for Atmospheric Research website (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>). The monthly NAO index is calculated based on the sea level pressure (SLP) difference between Ponta Delgada (Azores) and Stykkisholmur (Iceland), measured since 1865. NAO_w is estimated based on the SLP difference between Lisbon (Portugal) and Stykkisholmur between December and March, measured since 1864.

Meteorological data from 1987 to 2001 were obtained from the Royal Institute of Meteorology of Belgium. Daily rainfall (mm d^{-1}) corresponded to the average of 20 stations distributed in the Scheldt watershed. Wind speed (m s^{-1}) and direction (0–360°) data were taken at the coastal meteorological station of Middelkerke (Fig. 1) every 6 h. Southwesterly (SW) and northerly and easterly (N+E) winds were considered to be originating from sectors 180–270° and 270–180°, respectively. The magnitude of SW and N+E winds was calculated as the product of wind speed (m s^{-1}) and persistence (number of days) in each direction.

Data analysis—Long-term trend analysis from 1992 to 2000: Correlations between month-to-month variations of diatom biomass and climatic, meteorological, and hydrological variables were computed for monthly averaged data using a cumulative sum (Cusum) function (e.g., Beamish et al. 1999), thus:

$$\text{Cusum} = \sum_{t_i}^{t_f} (x_t - \bar{x}) \quad (1)$$

where x_t is the monthly averaged variable at time t (varying between initial t_i and final t_f), and \bar{x} is the variable averaged over the whole period of investigation. This function attributes less weight to single values. In Cusum plots, positive and negative slopes reflect increasing and decreasing trends, respectively. Prior to Cusum processing, monthly data were $\log(x + 1)$ -transformed to stabilize the variance and to give less weight to outliers. They were then deseasonalized using the Census I method (Makridakis et al. 1983). However, deseasonalization was not performed on the monthly NAO index and wind magnitude data, which do not display seasonal variation. Regression analysis was then conducted on Cusum data with Pearson coefficient analysis (SYSTAT Version 8, SPSS), and cross-correlation was used to detect a possible delayed effect. Statistical significance was set at $p < 0.05$. Degrees of freedom in the statistical tests were adjusted in order to remove autocorrelation (Pyper and Peterman 1998).

Interannual variability of spring blooms between 1988 and 2001: Because of the transient nature of *Phaeocystis* blooms compared to that of diatoms (Fig. 2), the use of Cusum was not relevant. The magnitude of *Phaeocystis* and diatom blooms was therefore estimated by integrating over time the phytoplankton data for the spring bloom period. Correlations were calculated between *Phaeocystis* and diatom spring blooms, NAO_w , wind magnitude, and the available nitrate stock. The latter was estimated by integrating concentrations between December and March–April (i.e., up to the date of *Phaeocystis* onset). Fitting of least-squares nonlinear regression was performed using Sigmaplot (Version 7, SPSS). Accuracy was evaluated based on r^2 , p values, and the pattern of residuals.

Results

Long-term trends: covariability of diatom biomass and monthly NAO index—Figure 3 compares the 1992–2000 monthly fluctuations and Cusum of diatom biomass at Sta. 330 (Fig. 3B) with those of the NAO index (Fig. 3A). The two series show a parallel trend, characterized by an increase between 1992 and 1995 until a maximum is reached, and a sharp decrease from 1995 to the end of 1998 (Fig. 3A,B). Thereafter, the two series diverge. Nevertheless, the regression between Cusum of diatom and NAO index is significant ($r^2 = 0.51$, $p < 0.001$, $n = 108$; Fig. 3C). The mechanisms behind this relationship are explored by investigating the links between NAO index variability and Cusum of meteorological (wind and

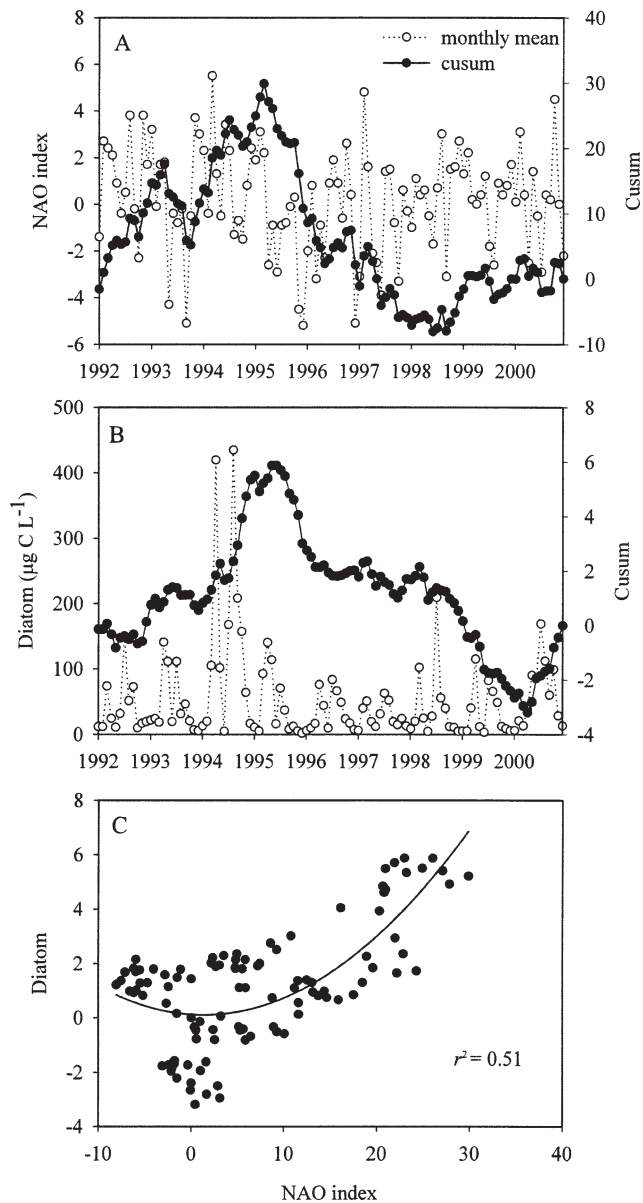


Fig. 3. 1992–2000 variations of monthly means and Cusum of (A) NAO index, (B) diatom biomass ($\mu\text{g C L}^{-1}$) at Sta. 330; (C) Relationship between Cusum of NAO index and diatom biomass.

rainfall) and hydrodynamical (ECWI in BCZ, Scheldt runoff and freshwater influence at Sta. 330) variables (Figs. 4, 5). The link between BCZ meteorological conditions and the NAO index is shown by the significant relationships between Cusum of wind dominance (expressed as the ratio between N+E and SW winds; (N+E) : SW), rainfall, and the NAO index (Fig. 4A,B). A decrease in (N+E) : SW is correlated to an increase in the NAO index ($r^2 = 0.77$, $p < 0.001$, $n = 108$; Fig. 4A) as a result of the intensification of SW winds (Hurrell 1995). A decrease in (N+E) : SW is also negatively correlated to rainfall on the Scheldt watershed ($r^2 = 0.80$, $p < 0.001$, $n = 108$; Fig. 4B). The effect of this wind dominance change on the BCZ water mass signature is indicated by a negative

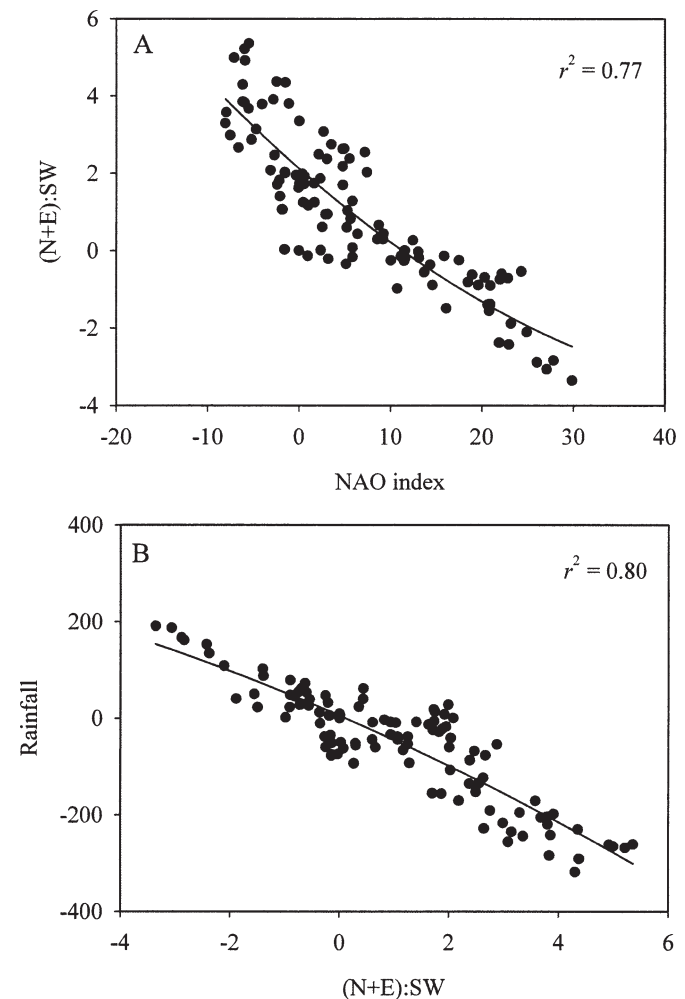


Fig. 4. Effect of NAO index on meteorological variables. Relationships between Cusum of (A) NAO index and (N+E) : SW and (B) (N+E) : SW and rainfall on the Scheldt watershed. (N+E) : SW represents the wind dominance and is expressed as the ratio of the magnitude of southwesterly (SW) and northerly + easterly (N+E) winds.

relationship between Cusum of ECWI and that of (N+E) : SW ($r^2 = 0.69$, $p < 0.001$, $n = 108$; Fig. 5A). On the other hand, correlation analysis between Cusum of Scheldt runoff and rainfall shows a positive link, with a 2-month delay ($r^2 = 0.83$, $p < 0.001$, $n = 106$; Fig. 5B). Wind direction in turn influences the spreading of the Scheldt plume at Sta. 330, as indicated by a significant positive relationship between Cusum of freshwater influence at Sta. 330 and (N+E) : SW ($r^2 = 0.87$, $p < 0.001$, $n = 72$; Fig. 6A). This relationship is further evidenced by a positive relationship between Cusum of SPM content at Sta. 330—an indicator of river influence—and (N+E) : SW ($r^2 = 0.67$, $p < 0.001$, $n = 72$; Fig. 6B). Surprisingly, Cusum of freshwater influence at Sta. 330 is negatively correlated to that of Scheldt runoff ($r^2 = 0.92$, $p < 0.001$, $n = 72$; Fig. 6C). This unexpected result is the consequence of two opposite phenomena. On the one hand, Scheldt runoff is positively related to the NAO index via rainfall on the Scheldt watershed (Fig. 5B). On the other hand, freshwater

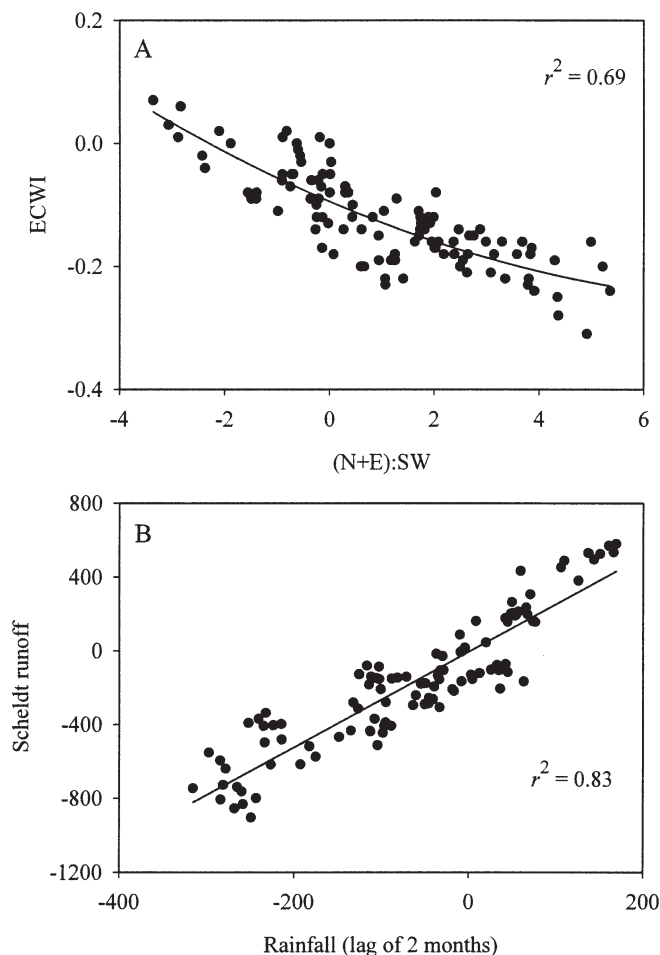


Fig. 5. Influence of local meteorological variables on hydrodynamical processes. Relationships between Cusum of (A) (N+E) : SW and the English Channel Water Inflow (ECWI) in BCZ and (B) rainfall and the Scheldt runoff, with a time lag of 2 months.

influence depends on (N+E) : SW, which is negatively correlated to rainfall (Fig. 4B). Together, these results strongly indicate that the long-term trend of diatom biomass at Sta. 330 is mostly related to a change in hydrodynamics (i.e., the balance between ECWI in the BCZ and freshwater inputs from the Scheldt).

Interannual variability of *Phaeocystis* and diatom spring blooms: The magnitude of spring *Phaeocystis* colony blooms between 1988 and 2001 indicates a nonlinear and nonmonotonic relationship with NAO_w ($r^2 = 0.44$, $p < 0.05$, $n = 14$; Fig. 7A). *Phaeocystis* blooms are positively related to negative NAO_w (Fig. 7A). For positive NAO_w , the trend is reversed (Fig. 7A). The relationship between the spring *Phaeocystis*-to-diatom biomass ratio (Phaeo : dia) and NAO_w is also nonlinear and nonmonotonic ($r^2 = 0.81$, $p < 0.001$, $n = 14$; Fig. 7B), with Phaeo : dia being negatively related to positive NAO_w but positively related to negative NAO_w (Fig. 7B). Interestingly, maximum Phaeo : dia at Sta. 330 is observed when NAO_w is close to 0 and corresponds to a significant *Phaeocystis* bloom (Fig. 7).

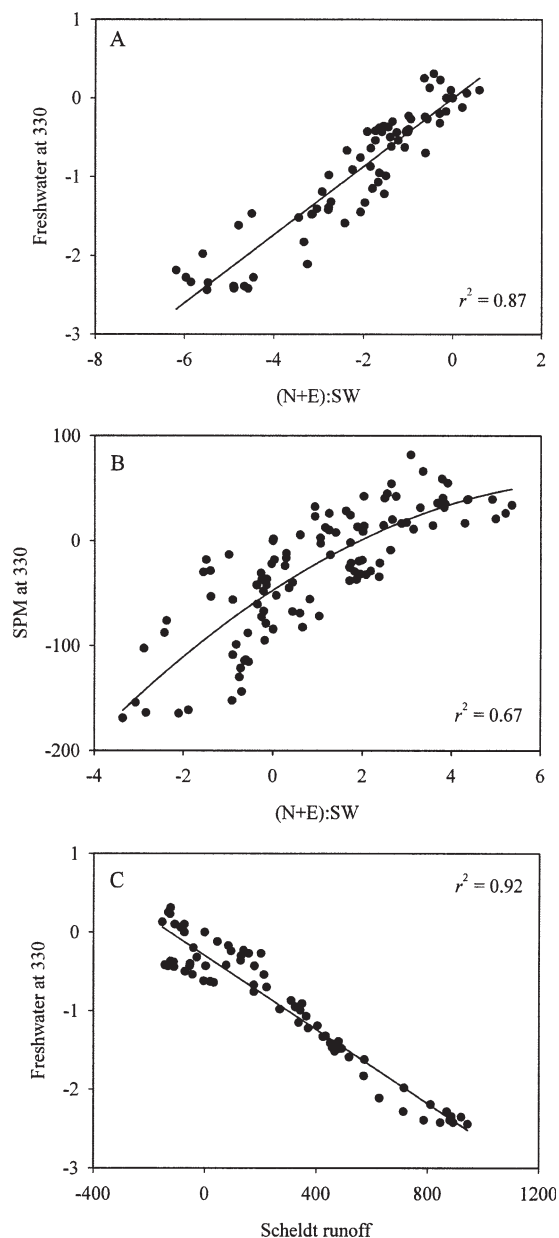


Fig. 6. Effect of wind regime on the spreading of the Scheldt plume at Sta. 330. Relationships between Cusum of (A) (N+E) : SW and freshwater influence at Sta. 330, (B) (N+E) : SW and SPM content at Sta. 330, and (C) Scheldt runoff and freshwater influence at Sta. 330.

The magnitude of *Phaeocystis* colony blooms also shows increasing and decreasing trends depending on whether (N+E) : SW is < 1 or > 1 ($r^2 = 0.74$, $p < 0.001$, $n = 14$; Fig. 8A). Likewise, Phaeo : dia depends on the (N+E) : SW according to a nonlinear and nonmonotonic relationship ($r^2 = 0.66$, $p < 0.001$, $n = 14$; Fig. 8B), with a slope disruption when (N+E) : SW is close to 1 (Fig. 8B). An analogous nonlinear and nonmonotonic relationship is observed between winter nitrate stocks at Sta. 330 and winter (N+E) : SW, with a reversed trend when the wind ratio approaches 1 ($r^2 = 0.61$, $p < 0.01$, $n = 13$; Fig. 9A). The latter relationship results from the combined and opposite

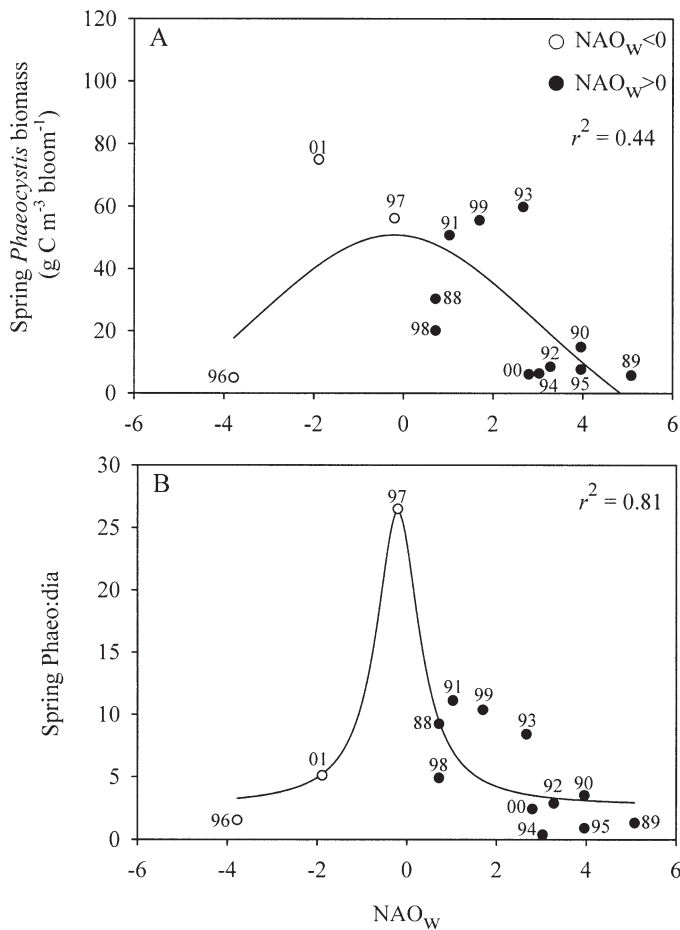


Fig. 7. Relationships between NAO_w and (A) the magnitude of *Phaeocystis* colonies ($g\ C\ m^{-3}\ bloom^{-1}$) and (B) the Phaeo : dia spring biomass ratio at Sta. 330. Solid lines represent Lorentzian model fits.

effect of the wind regime on Scheldt runoff and plume spreading (Fig. 6A,C). Interestingly, this relationship was not found to be significant for other nutrients (phosphate: $r^2 = 0.23$, $p > 0.05$; silicate: $r^2 = 0.02$, $p > 0.05$). Finally, a nonlinear but monotonic relationship is found between *Phaeocystis* colony blooms and winter nitrate enrichment at Sta. 330 ($r^2 = 0.53$, $p < 0.01$, $n = 13$; Fig. 9B).

Discussion

Whether long-term changes in *Phaeocystis* colony blooms in the Southern Bight of the North Sea are due to climate (Owens et al. 1989) and/or human-induced nutrient enrichment of coastal waters (Cadée and Hegeman 1991) is still the subject of debate. Our statistical analysis of 1988–2001 phytoplankton records in BCZ at Sta. 330 in relation to hydro-meteorological data and Scheldt River loads provides the first evidence of a synergy between climate and human-induced river-based nitrate inputs with respect to their effects on the magnitude of spring *Phaeocystis* colony blooms and their dominance over diatoms (Fig. 10). There appears to be a complex cascade of natural events entangled with human activity in the

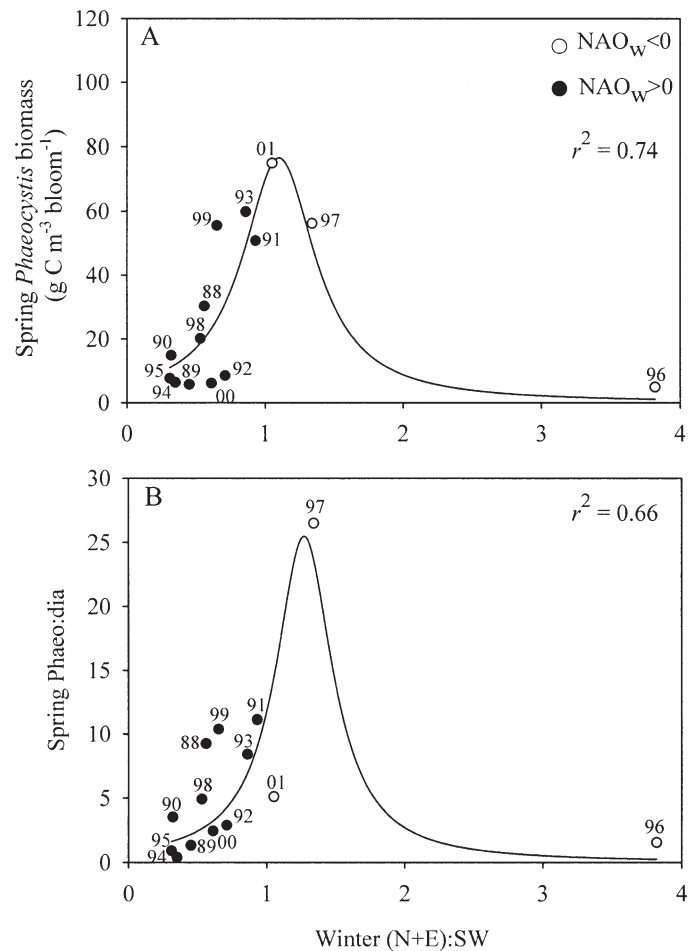


Fig. 8. Relationships between winter (N+E) : SW and (A) the magnitude of *Phaeocystis* colonies ($g\ C\ m^{-3}\ bloom^{-1}$) and (B) phytoplankton composition at Sta. 330. Solid lines represent Lorentzian model fits.

watershed. The primary effects of climate variability are local wind dominance and rainfall in the Scheldt watershed, which determine water dynamics and budgets in the BCZ. Meteorological conditions, in turn, modulate the spreading in BCZ of continental nitrates discharged by the Scheldt. That ultimately influences the magnitude of spring *Phaeocystis* blooms at Sta. 330, as well as their dominance over diatoms (Fig. 10). Indeed, by constraining rainfall and wind, the NAO affects nitrate inputs (as a result of the positive link between nitrate loads and runoff) and their spreading in the coastal area. This process in turn influences the winter nutrient level and, ultimately, phytoplankton communities at Sta. 330 (Fig. 10).

Our results agree with current knowledge of the NAO's effect on marine phytoplankton dynamics and community structure, both in oceanic and coastal areas of the North Sea and Northeast Atlantic waters (e.g., Drinkwater et al. 2003). However, most previous studies show a linear relationship between NAO and plankton. Our results clearly indicate a nonlinear and nonmonotonic response of phytoplankton to NAO. Indeed, diatoms are positively (negatively) related to positive (negative) NAO variations (Fig. 3C). The

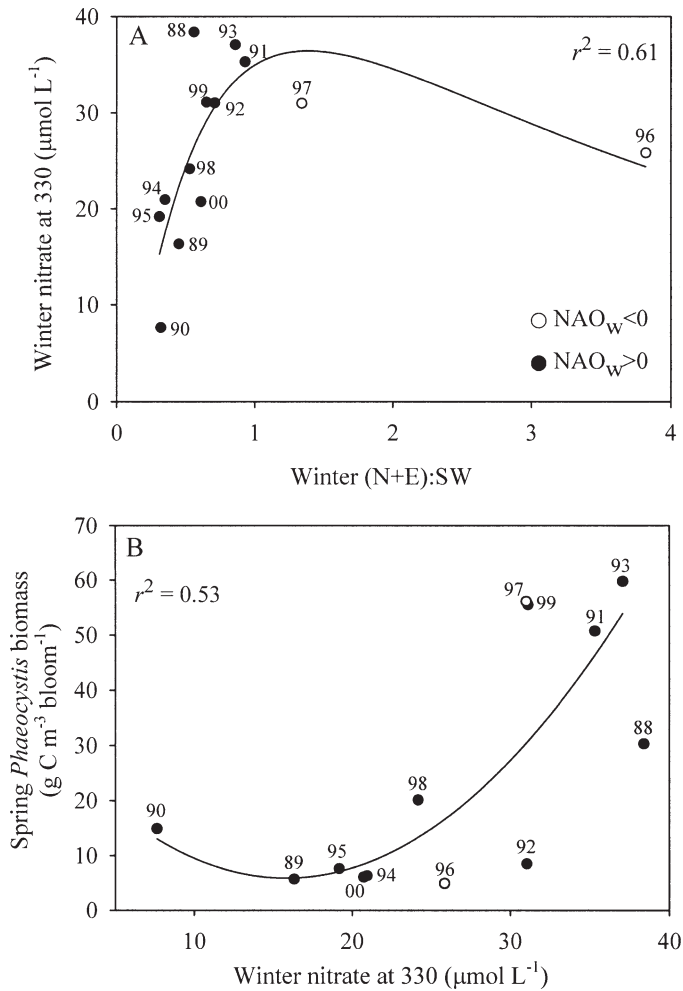


Fig. 9. Relationships between (A) winter (N+E) : SW and winter nitrate concentrations at Sta. 330 and (B) winter nitrate concentrations and spring *Phaeocystis* colony bloom ($\text{g C m}^{-3} \text{ bloom}^{-1}$) at Sta. 330. Solid lines represent (A) Log-normal and (B) quadratic model fits.

dominance of *Phaeocystis* over diatoms is negatively related to positive NAO_w values, but the reverse holds for negative NAO_w values (1996, 1997, and 2001; Fig. 7B).

Mysterud et al. (2003) demonstrated nonlinear and nonmonotonic effects of climate variability on terrestrial biology. They also suggested that the response of marine organisms to climate variability could be explained by a nonlinear relationship between climate variability and meteorological conditions and/or a nonlinear response of biology to local climate variability. In our case study, the nonlinear relationship between phytoplankton and climate variability results from the opposite NAO modulation of Scheldt freshwater and nitrate discharge, on the one hand, and their spreading in the BCZ on the other hand. Indeed, high NAO values (>2) are associated with high rainfall and river runoff, which results in high Scheldt nitrate inputs to the BCZ (Fig. 10A). However, because high NAO values are also related to the dominance of SW over N+E winds, they drive the spreading of the Scheldt plume into a northeasterly direction, which consequently reduces (or

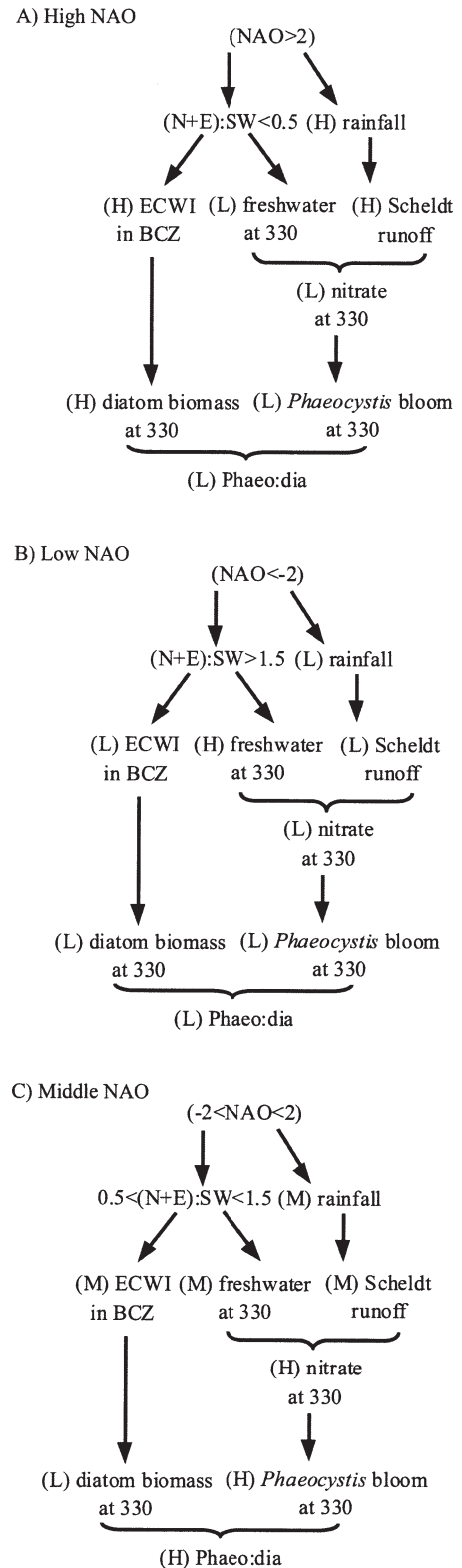


Fig. 10. Mechanisms linking NAO, meteorological, hydro-dynamical, and physico-chemical parameters and diatom and *Phaeocystis* spring blooms at Sta. 330 under (A) high NAO, (B) low NAO, and (C) middle NAO. H, L, and M refer to high, low, and middle, respectively.

prevents) the spreading of Scheldt nitrates to Sta. 330 (Fig. 10A). Therefore, during high NAO years, nitrate loads at Sta. 330 are low and *Phaeocystis* blooms are expected to be less important (Fig. 10A). Low NAO years (<-2) also generate low *Phaeocystis* blooms, but that is due to NAO-driven low Scheldt runoff (Fig. 10B). Therefore, our results indicate that the conditions for intense *Phaeocystis* blooms at Sta. 330 are those for which Scheldt runoff and plume spreading do not offset each other (i.e., when these two parameters display average conditions, which coincides with $0.5 < (N+E) : SW < 1.5$ (Fig. 10C).

Temperature and wind conditions are often mentioned as factors underlying the relationship between phytoplankton and the NAO in oceanic regions (Drinkwater et al. 2003). However, in our coastal station, the significant relationship obtained between spring *Phaeocystis* bloom magnitude and winter nitrate concentrations indicates that nitrate enrichment is the principal factor regulating the magnitude of *Phaeocystis* blooms and phytoplankton community. This result is consistent with those of previous studies that demonstrate a positive link between *Phaeocystis* cell density and nitrate excess after the early spring diatom bloom controlled by phosphate and silicate availability (Lancelot et al. 1998; Rousseau 2000).

Phaeocystis is known to be able to grow on organic sources of phosphorus when phosphate is depleted (van Boekel and Veldhuis 1990) and in springtime when dissolved organic phosphorus is abundant (Van der Zee and Chou 2004). In the central and northern North Sea and western Swedish coastal waters, high NAO has been suggested to increase the contribution of flagellates (nonsiliceous phytoplankton) over diatoms (Drinkwater et al. 2003). However, the opposite result was reported for English Channel coastal waters (Irigoien et al. 2000). Our analysis confirms these observations, as it indicates a decreasing importance of *Phaeocystis* at Sta. 330 during high NAO years. These opposite conclusions on the effect of NAO fluctuations on the North Atlantic phytoplankton community indicate specific regional responses. These regional differences are not due to local meteorological conditions (Hurrell and Dickson 2004) but rather to the way local wind and rainfall affect hydrodynamics and nutrient loads. Because of these geographical peculiarities, a deeper understanding of the causal mechanisms linking NAO and phytoplankton is required before concluding that there is a common rule that determines phytoplankton structure over large areas (e.g., Stenseth et al. 2002). Finally, our results point to the importance of the choice of monitoring stations for studying eutrophication in coastal areas such as the BCZ, where the geographical extent of river loads is highly variable, depending in a complex and opposite way on wind direction and rainfall, both of which are driven by NAO.

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Received: 9 June 2005

Amended: 5 December 2005

Accepted: 7 December 2005