

ABIOTIC DRIVERS OF INTERANNUAL PHYTOPLANKTON VARIABILITY AND A 1999–2000 REGIME SHIFT IN THE NORTH SEA EXAMINED BY MULTIVARIATE STATISTICS¹

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The Dutch coastal zone is a region of the North Sea with a marked interannual and long-term abiotic and phytoplankton variability. To investigate the relationship between abiotic variability and phytoplankton composition, two routine water monitoring data sets (1991–2005) were examined. Multivariate statistics revealed two significant partitions in the data. The first consisted of interannual abiotic fluctuations that were correlated to Rhine discharge that affected the abundance of summer and autumn diatom species. The second partition was caused by a shift in the abiotic data from 1998 to 1999 that was followed by a shift in phytoplankton composition from 1999 to 2000. Important factors in the abiotic shift were decreases in suspended matter (SPM) and phosphate (DIP) concentrations, as well as in pH. The decrease in SPM was caused by a reduction in wind speed. The increase in water column daily irradiance from the decrease in SPM led to increases in the abundance of winter–spring species, notably the prymnesiophyte *Phaeocystis globosa*. Because wind speed is related to the North Atlantic Oscillation (NAO) index it was possible to correlate NAO index and *P. globosa* abundance. Only five abiotic variables representing interannual and long-term variability, including Rhine discharge and NAO index, were needed to model the observed partitions in phytoplankton composition. It was concluded that interannual variability in the coastal phytoplankton composition was related to year-to-year changes in river discharge while the long-term shift was caused by an alternating large-scale meteorological phenomenon.

Key index words: climate change; diatom; light; nutrients; ocean acidification; phytoplankton; salinity

Abbreviations: AIC, Akaike information criterion; dbRDA, distance-based redundancy analysis; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; DISTLM, distance-based linear model; E_0 , daily surface irradiance; E_m , water column mean daily irradiance; K_d , irradiance attenuation coefficient; NAO, North Atlantic Oscillation; NMS, nonmetric multidimensional scaling; PCO, principal

coordinate analysis; PERMANOVA, permutational multivariate analysis of variance; PERMDISP, distance-based test for homogeneity of multivariate dispersions; PRIMER, plymouth routines in marine ecology; SPM, suspended matter

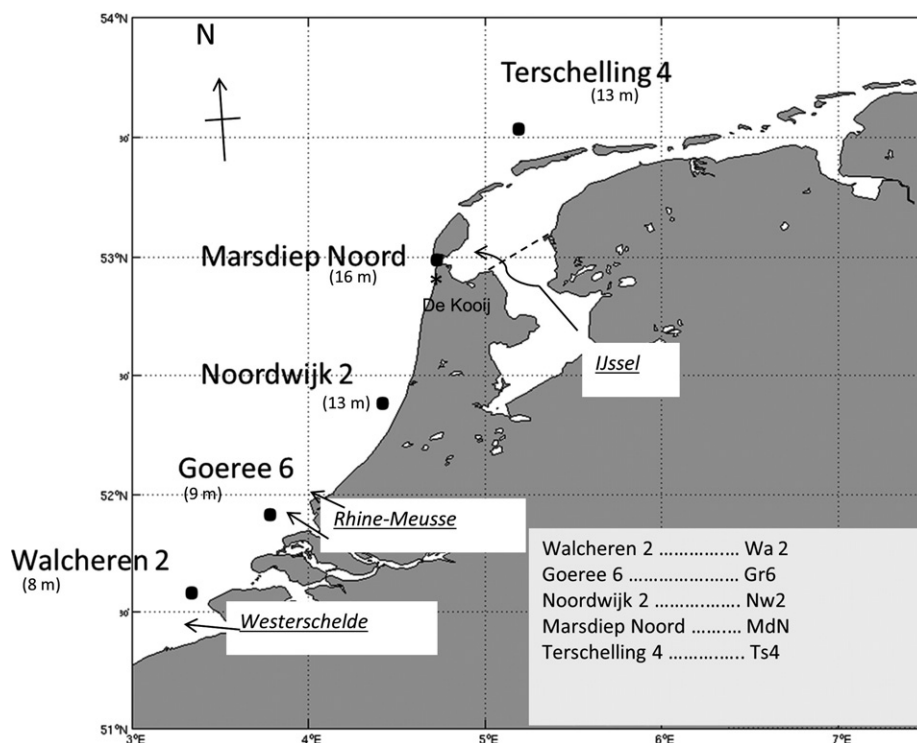
The Dutch coastal zone is a region of the North Sea where interannual and long-term abiotic aquatic variability is related to both natural and anthropogenic factors. At one station, the Marsdiep (Fig. 1) water temperature increased by $\sim 1.5^\circ\text{C}$ since 1982 due to changes in wind statistics and cloudiness (van Aken 2008b). Long-term changes in atmospheric forcing may be related to the North Atlantic Oscillation (NAO). The NAO refers to a redistribution of atmospheric mass between the Arctic and the subtropical Atlantic. Its index of pressure difference, with no apparent pattern, coherently fluctuates with surface pressure, temperature, cloudiness, and precipitation throughout the year over the North Atlantic as well as on adjacent continents (Hurrell and Deser 2009). The salinity in the Marsdiep depends mainly on Rhine discharge, weather conditions, and wind direction (van Aken 2008a). The suspended matter budget of the coastal zone is dominated by the amount of clay, silt, and sand that enters the North Sea through the Dover Strait and variations in Rhine discharge. In addition, Belgian and Dutch coastal engineering works between 1969 and 1986 and the disposal of Rotterdam harbor dredge since 1970 increased suspended matter concentrations (Van Alphen 1990, de Jonge and de Jong 2002).

Nutrient-rich freshwater discharged by the rivers Westerschelde, Rhine-Meuse, and IJssel (Fig. 1) is mixed with northward flowing seawater leading to gradients in salinity and nutrients perpendicular to and along the Dutch coast (van Bennekom and Wetsteijn 1990, Peeters et al. 1991). In addition, perpendicular gradients in turbulence and in water column irradiance are also observed due to the off-shore increase in water depth (Gieskes and Kraay 1975, Peeters et al. 1991, Peperzak 1993). The nutrient concentrations in the Dutch coastal zone are determined largely by nutrient loads from the Rhine. Eutrophication in this area started in the 1960s (van Bennekom and Wetsteijn 1990) and led to an enhancement of phytoplankton biomass

¹Received 14 September 2018. Accepted 17 May 2019. First Published Online 17 June 2019. Published Online 24 August 2019, Wiley Online Library (wileyonlinelibrary.com).

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Editorial Responsibility: M. Roleda (Associate Editor)

FIG. 1. Five monitoring stations closest to the coast of The Netherlands, in the text abbreviated as Wa2, Gr6, Nw2, MdN, and Ts4. Station MdN is located in the tidal inlet to the Wadden Sea. Numbers in parenthesis are depths in meters. The average depth is 12 m. * is meteorological station De Kooy for wind and irradiance data. The mean residual current along the coast is north-east. Standard area D1 of the Continuous Plankton Recorder survey has the same geographical borders but extends 1° to the north (55°). The Belgian coastal zone is located south of Walcheren 2.



(Gieskes and Schaub 1990, Peeters et al. 1991). Between 1970 and 1990 the phosphate loads of the Rhine declined by a factor of three while the nitrogen loads started to decline after 1990 (Vermaat et al. 2008). Despite the considerable reduction in phosphate loads chlorophyll-*a* concentrations remained high till at least 1995 (de Vries et al. 1998). This may be due to the finding that water transparency in winter and the annual mean sea surface temperature, not nutrient concentrations, are the most probable predictors of coastal North Sea chlorophyll-*a* concentrations (McQuatters-Gollop et al. 2007).

Despite past extensive studies of Rhine-related eutrophication of the North Sea in terms of nutrient and chlorophyll-*a* concentrations, surprisingly little investigations have been conducted on the combination of spatial gradients and interannual trends in abiotic factors and how these trends affect the local phytoplankton community structure. The combined spatial and seasonal changes in phytoplankton species composition in the Dutch coastal zone of the North Sea have only been described for the year 1974 (Gieskes and Kraay 1975, Leewis 1985). All other phytoplankton research in this region was dedicated to the dynamics of specific groups such as diatoms, flagellates, bloom-forming or potentially harmful algae, and were restricted to particular seasons of the year (Kat 1982a,b, 1989, 1992, Veldhuis et al. 1986a,b, Vrieling et al. 1995, Peperzak et al. 1996, 1998, Rademaker et al. 1997, de Boer 2006, Blauw et al. 2010, Van der Woerd et al. 2010).

Phytoplankton is the autotrophic intermediate between the abiotic environment and the heterotrophic

food chain. How changes in abiotic variables affect the variability in phytoplankton composition and biomass is an important research topic because phytoplankton variability, in turn, may affect higher trophic levels of the ecosystem (Beaugrand et al. 2003, Cloern and Dufford 2005, Philippart et al. 2007). However, a major problem in comparing abiotic and biotic data such as phytoplankton community structure is based on the fact that both data sets are multivariate. They consist of multiple variables (e.g., nutrient concentrations, salinity and temperature, and an assemblage of phytoplankton species). These data are difficult to correlate directly with each other in a meaningful way (e.g., by correlating all variables one to one with all individual phytoplankton species). In addition, phytoplankton data sets as ecological data sets, in general, may consist of large numbers of zero counts which necessitate a specific treatment of such data before statistical analysis can take place. Therefore, specific multivariate statistical tools are needed to examine, plot, and correlate multivariate biotic and abiotic data (Clarke and Warwick 2001, McCune and Grace 2002, Anderson et al. 2008).

Here the first pluriannual, multivariate phytoplankton analysis in relation to multivariate abiotic data for the Dutch coastal zone of the North Sea is reported. The aim was to investigate if the phytoplankton community structure could be explained by the aquatic abiotic data (temperature, salinity, nutrients, suspended matter, pH, and daily water column irradiance). The general null hypotheses investigated are that there is no relation among

abiotic variables and no relation between abiotic variables and phytoplankton species composition. However, the effects of interannual variability and long-term changes and their effect on the phytoplankton community were discovered. Which abiotic variables and phytoplankton species were involved was further examined in time-series diagrams and linear regression. Major factors in short and long-term variability were salinity (Rhine discharge) and wind speed (NAO index). Finally, a model including Rhine discharge and NAO was made that successfully calculated the observed short- and long-term phytoplankton development.

METHODS

Data. Data were extracted from abiotic and phytoplankton databases from the Dutch monitoring authority Rijkswaterstaat (live.waterbase.nl/). The five monitoring stations along and closest to the Dutch coast were chosen (Fig. 1). The years 1991–2005 (first 15 years) of phytoplankton monitoring were selected for analyses so that after 2020 a second batch of 15 years time-series data can be used for an independent check of the models built in the present study. From the phytoplankton data set (species · L⁻¹), 10 easily recognized species were selected that should have been counted in every sample, if present, by the various Rijkswaterstaat subcontractors that performed the phytoplankton analysis (Table 1). This way, the observer effect, the effect of different phytoplankton counters, that is present in the complete data set is avoided (Peperzak 2010).

Abiotic variables consisted of salinity (Sal), temperature (T, °C), pH, dissolved inorganic nitrogen (DIN, µM) and phosphorus (DIP, µM), silicate (Si, µM), suspended matter (SPM, mg · L⁻¹), and chlorophyll-*a* (Chl*a*, µg · L⁻¹). Chlorophyll-*a* was only used for modeling the irradiance attenuation coefficient.

Data preparation. Because some months were sampled once (October to March) and others twice per month (April–

September) both phytoplankton and abiotic variables were averaged by month. The final data set consisted of two equally structured matrices with observations for five locations, 15 years, and 12 months ($n = 900$). Missing values, due to a missing sample, were calculated by linear interpolation.

The irradiance attenuation coefficient (K_d , m⁻¹) was modeled by month, assuming shallow (Fig. 1) mixed water columns as (Peperzak et al. 1998):

$$K_d = 2.404 - 0.058 * \text{Sal} + 0.012 * \text{SPM} + 0.020 * \text{Chl}a \quad (1)$$

and the water column mean daily irradiance as (Peperzak 1993):

$$E_m = E_0 \times (1 - e^{-K_d \times z}) / (K_d \times z) (\text{mol photons} \cdot \text{m}^{-2} \cdot \text{d}^{-1}) \quad (2)$$

Daily surface irradiance (E_0) and wind speed data were obtained from the Dutch Meteorological Institute, location De Kooy (Fig. 1; <http://www.knmi.nl>). Rhine discharge data from the Rhine/Meuse (Maassluis and Haringvliet) were obtained from Rijkswaterstaat. The annual principal component-based NAO index was retrieved from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>.

Multivariate abiotic and phytoplankton data analysis was performed in PRIMER (Plymouth Routines in Marine Ecology) version 6.1.13 with PERMANOVA+ version 1.0.3 as an add-in. Traditional PRIMER analyses are based on ranked distances between samples calculated in (dis)-similarity matrices. On the other hand, in PERMANOVA+ the similarity matrices should preserve the distances between samples because it partitions the variance among categorical (e.g., Permutation MANOVA or PERMANOVA) or continuous predictor variables (e.g., distance-based linear models or DISTLM).

For initial data analysis PRIMER was used for data transformations, the calculation of similarity matrices, rank-based ordinations (nonmetric multidimensional scaling, NMS), and the test of no correlation between similarity matrices (RELATE, 2nd STAGE NMS). Abiotic data were square root-transformed to reduce skewness and outliers as was checked in Draftsman plots. To scale the data, as is usual in ecological data sets, phytoplankton abundances were $\log(x + 1)$ transformed.

In PERMANOVA+ the distances between samples in the similarity matrices should be symmetrical, which was checked in the Shepard plots that are produced during the construction of NMS ordinations. The Shepard plot for the abiotic data ($n = 900$) based on Euclidean distances showed a relatively symmetrical distribution of distances. However, due to zero abundances in the phytoplankton data, the standard Bray–Curtis matrix could not be used and that data, as well as the abiotic data, was further averaged by season ($n = 300$). The seasons were based on a Bray–Curtis matrix and NMS of monthly averaged phytoplankton data with the winter season starting in December of the previous year (see results).

Even after averaging by season, a few zero abundances in the phytoplankton data remained and a dummy variable (1 instead of 0) was used in the calculation of the Bray–Curtis matrix: a Shepard plot showed that sample distances were now symmetrically distributed. In the analyses of further averaged data, such as by location or by year, where zero abundances vanished, a Bray–Curtis matrix without a dummy variable was used.

Statistical calculations. For a first test of the null hypothesis that there is no relation between abiotic variables and phytoplankton, two similarity matrices for the seasonally averaged ($n = 300$) data were calculated: a Euclidean matrix for the

TABLE 1. Selected phytoplankton species, abbreviations used in ordinations, taxonomic affiliation, and the approximate seasonal appearance according to Figure 2.

Species	Abbreviation	Taxonomy	Season
<i>Asterionella glacialis</i>	Agla	Diatom-pennate	Spring
<i>Leptocylindrus danicus</i>	Ldan	Diatom-centric	Autumn
<i>Odontella sinensis</i>	Osin	Diatom-centric	Summer
<i>Paralia marina</i>	Pmar	Diatom-pennate	Winter
<i>Phaeocystis globosa</i>	Pglo	Prymnesiophyte	Spring
<i>Rhizosolenia delicatula</i>	Rdel	Diatom-centric	Summer
<i>Rhizosolenia setigera</i>	Rset	Diatom-centric	Spring–summer
<i>Rhizosolenia shrubsolei</i>	Rshr	Diatom-centric	Summer
<i>Thalassionema nitzschioides</i>	Tnit	Diatom-pennate	Winter
<i>Torodinium robustum</i>	Trob	Dinoflagellate	Spring

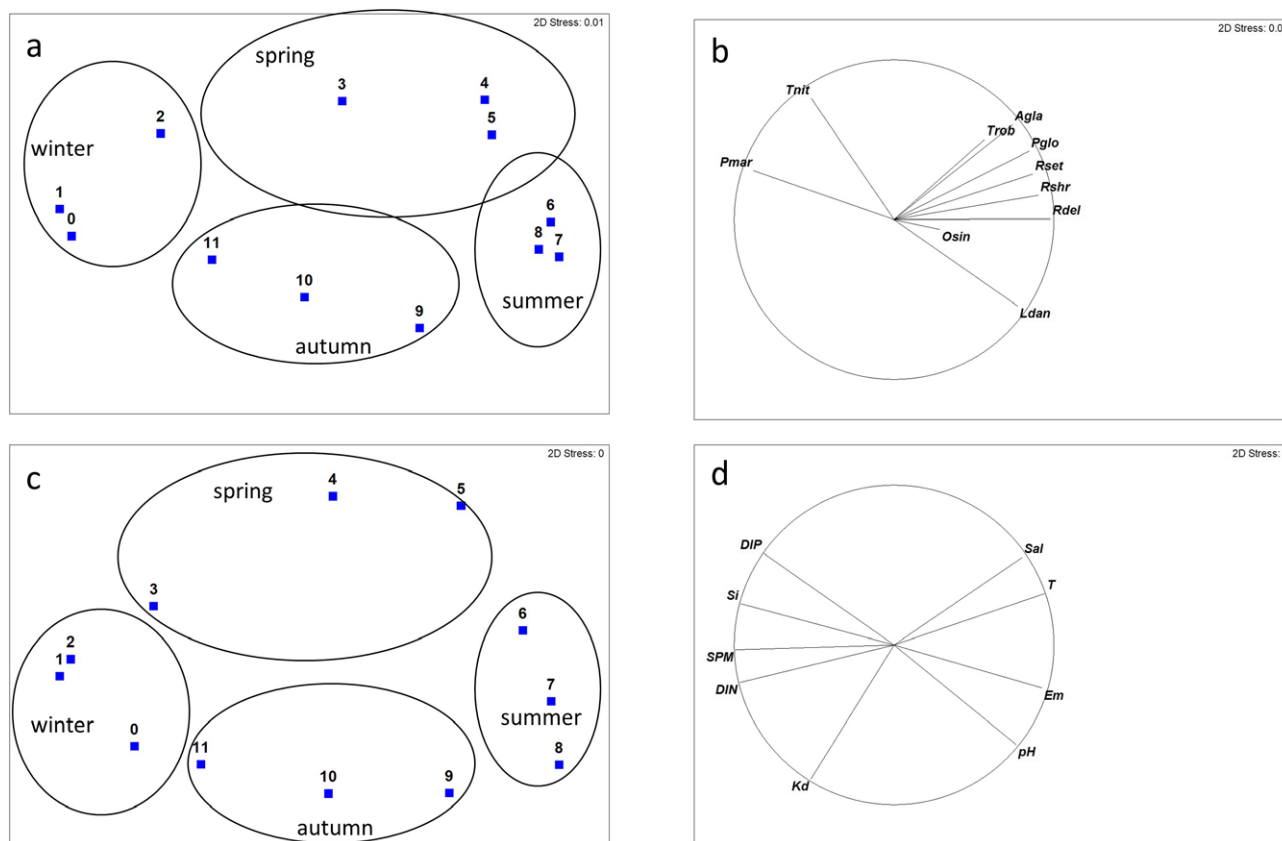


FIG. 2. NMS ordinations of monthly changes in phytoplankton composition and abiotic data. The months are numbered from 0 (December of the previous year) to 11. (a) Abiotic ordination showing strong seasonality. (b) Abiotic vector plot with the nine abiotic variables: Sal = salinity, T = temperature, E_m = water column irradiance, K_d = attenuation coefficient, DIN and DIP = dissolved inorganic nitrogen and dissolved inorganic phosphorus, SPM = suspended particulate matter, Si = silicate. Winter months (left) are characterized by high nutrient and SPM concentrations. Summer months (right) have a high water column irradiance (E_m), temperature and salinity. (c) Phytoplankton ordination with four seasonal clusters (ellipses drawn by hand). (d) Phytoplankton vector plot with 10 species underlying the seasonal pattern (abbreviations see Table 1). [Color figure can be viewed at wileyonlinelibrary.com]

abiotic data (after normalization) and a Bray–Curtis matrix (dummy = 1) for the phytoplankton data, followed by PRIMER's RELATE with 999 permutations and a Spearman rank correlation test.

First, to examine autocorrelation between years, the strength of the seasonality was calculated for both the abiotic and the phytoplankton matrices in a RELATE test based on cyclicity with 999 permutations and a Spearman rank correlation test. A RELATE test was also used to calculate the seasonal correlation between the abiotic and phytoplankton matrices.

Second, a PERMANOVA model was constructed to examine the significance of the main factors years, seasons, and locations for both the abiotic and the phytoplankton data ($n = 300$). Years and locations were chosen as random factors, the seasons were fixed factors. Type III sum of squares and permutation of residuals ($n = 999$) were used under a reduced model. Due to significant interactions between the three main factors, two-factor models were calculated for both data sets using the same settings as for the three-factor model. Because only year and location did not interact (see results) the third step was an analysis of both datasets by location (after averaging all years) and by year (after averaging all locations).

In step number three, the differences between the locations and the years were visualized by PCO analysis, an analog of principal component analysis (PCA) but not restricted to

Euclidean (abiotic) distance matrices (Anderson et al. 2008). The transformed abiotic and phytoplankton data ($n = 300$) was averaged by location ($n = 5$) or by year ($n = 15$) and projected on two PCO axes after calculation of Euclidean and Bray–Curtis matrices. Vectors of individual variables were plotted in each PCO.

PERMANOVA was used to examine the significance of differences between groups of years using type III sum of squares and unrestricted permutation of raw data ($n = 999$). In addition, PERMDISP (Distance-based test for homogeneity

TABLE 2. PERMANOVA of the abiotic and phytoplankton data. Not only are the main factors highly significant, this is also the case for the interaction terms.

Source	df	Abiotics		Phytoplankton	
		Pseudo- F	P	Pseudo- F	P
Location	4	56.3	<0.001	5.4	<0.001
Year	14	6.1	<0.001	2.8	<0.001
Season	3	72.4	<0.001	28.1	<0.001
Location \times year	56	1.9	<0.001	1.9	<0.001
Location \times season	12	2.6	<0.001	2.5	<0.001
Year \times season	42	2.6	<0.001	3.2	<0.001

of multivariate dispersions), a complement to PERMANOVA, was used to test the null hypothesis of no differences in the within-group multivariate dispersion among groups using distances to centroids and P-values from permutation ($n = 999$) (Anderson et al. 2008).

Fourth, individual abiotic and phytoplankton variables were examined in time-series diagrams. Linear regression lines with the adjusted and squared correlation factors were calculated in SYSTAT 13. Pearson correlations between variables were also calculated in SYSTAT 13.

Fifth, the relation between the multivariate phytoplankton data set and one or more predictor variables was investigated using distance-based linear modeling (DISTLM) in PRIMER using the BEST selection procedure, the AIC selection criterion, and 999 permutations. Annual averages of NAO index, wind speed, and Rhine discharge were added to the abiotic dataset ($n = 12$). DISTLM partitions the variation in the phytoplankton resemblance matrix according to a stepwise multiple regression model (Anderson et al. 2008). The value of AIC will not increase with an increasing number of predictor variables in the model as does r^2 (Anderson et al. 2008). K_d and salinity were excluded because of strong autocorrelations with SPM and with Rhine discharge respectively (see results). The fitted model was visualized by using distance-based redundancy analysis (dbRDA).

RESULTS

Four phytoplankton seasons were identified based on a strong cyclic pattern (RELATE $\rho = 0.71$, $P < 0.001$; Fig. 2a) with each year starting in December of the previous year and ending in November.

The 10 selected species were representative for winter to autumn species (Fig. 2b). The strong seasonality in the phytoplankton composition indicates that a “reset” takes place every winter (i.e., that there is no autocorrelation between years). In addition, the abiotic data also showed a strong cyclic pattern (RELATE $\rho = 0.80$, $P < 0.001$; Fig. 2c). Both abiotic and phytoplankton cyclic patterns were strongly correlated (RELATE $\rho = 0.82$, $P < 0.001$). Winter conditions were characterized by high nutrient and SPM concentrations, summer conditions by high temperature, salinity, and water column daily irradiance (Fig. 2d).

The null hypothesis that there is no relation between abiotic variables and phytoplankton species in the total data set was rejected: the correlation between all nine abiotic and all 10 phytoplankton variables was significant: $\rho = 0.49$ ($P < 0.001$).

PERMANOVA analyses of the abiotic and phytoplankton data with location, year, and season revealed significant interactions between all factors (Table 2). In the phytoplankton data, significant interactions remained between year and season and between location and season, but not between year and location (results not shown). Therefore, the next step was to perform a PCO analysis of both datasets by location and year separately.

The PCO analyses showed differences among locations in both abiotic and in phytoplankton

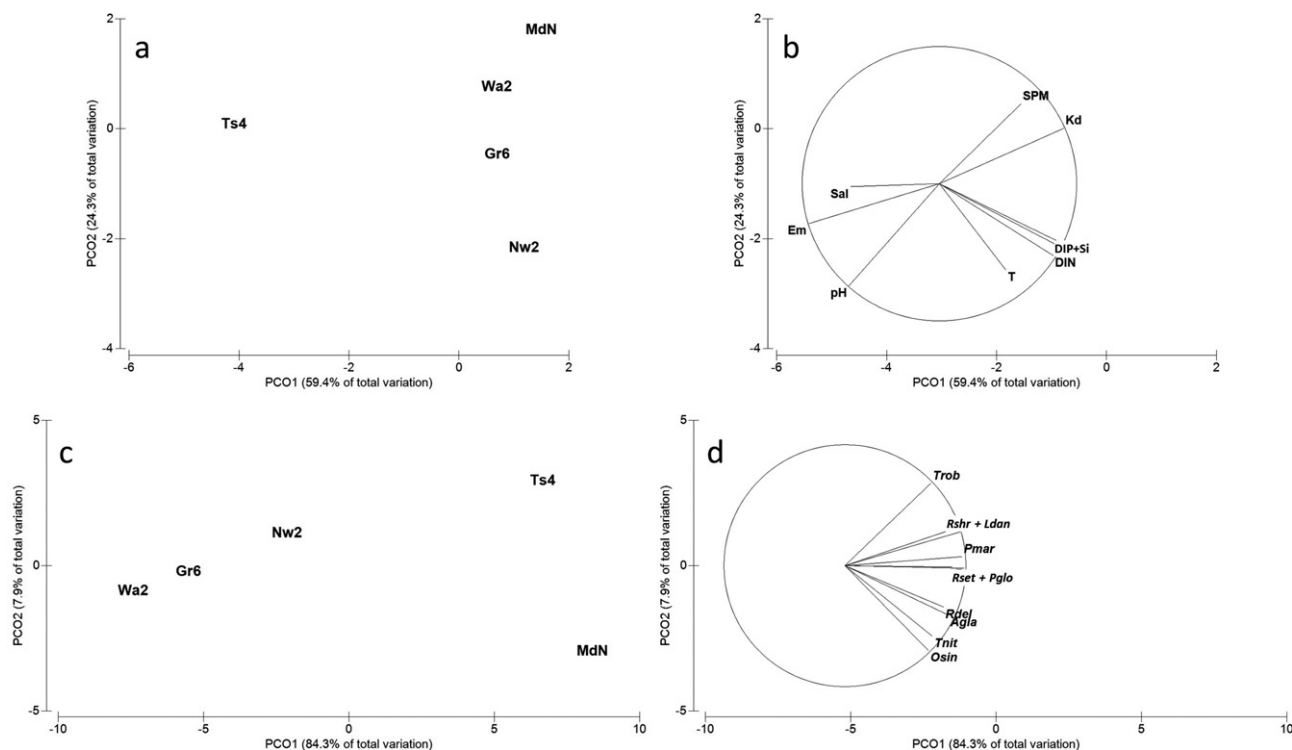


FIG. 3. Principal coordinate (PCO) diagrams for the abiotic (a, b) and phytoplankton (c, d) data averaged for five coastal locations. The vector plots (b, d) show individual variables. Ts4 differs considerably in abiotic variables (a) while MdN is not part of the Wa2 to Ts4 phytoplankton sequence (c).

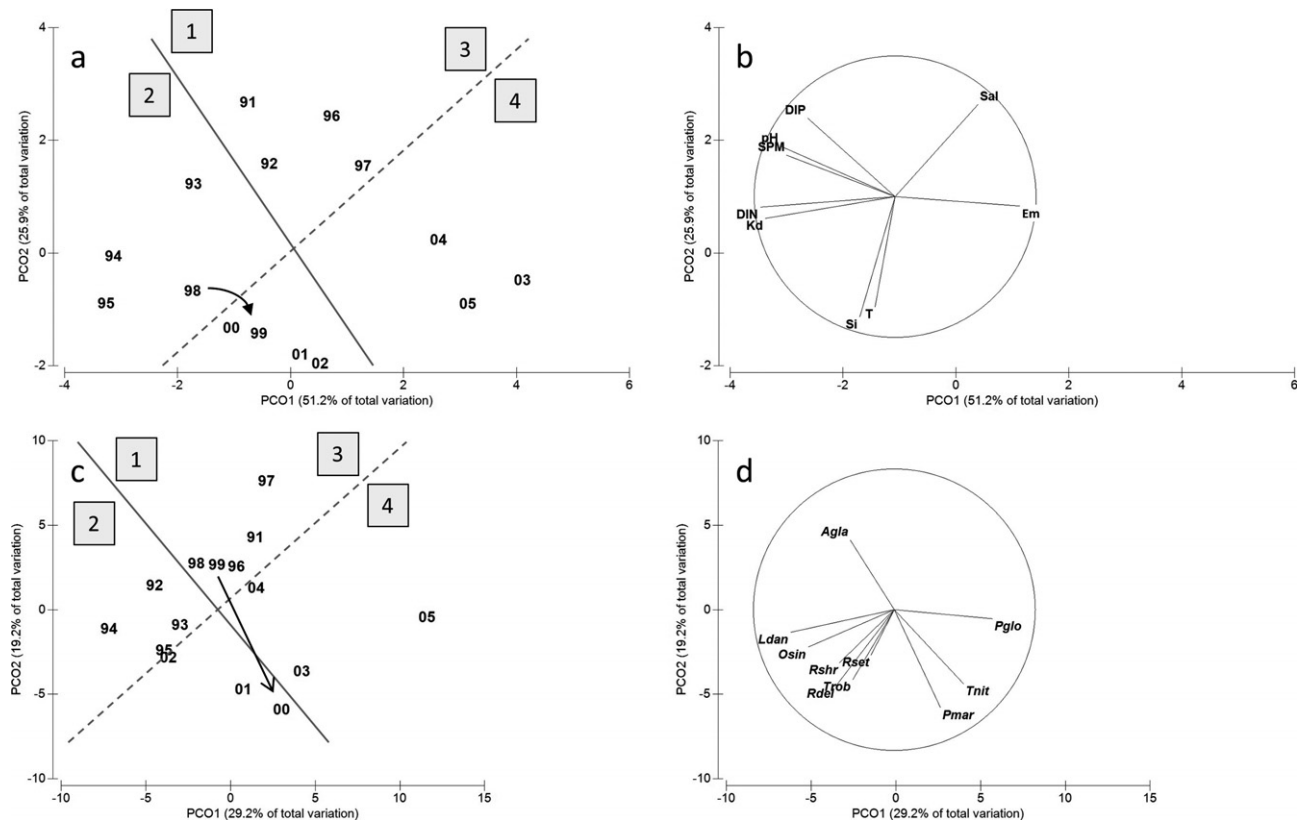


FIG. 4. Principal coordinate (PCO) diagrams for the abiotic (a, b) and phytoplankton data (c, d). The numbers designate years (1991–2005). The vector plots (b, d) show the individual variables underlying the ordinations. Two partitions can be made. In the abiotic data (a) group 1 and 2 are separated according to interannual differences and group 3 and 4 by a long-term shift from 1998 to 1999. In the phytoplankton data (b) group 1 and 2 are also separated according to interannual differences and group 3 and 4 by a long-term shift from 1999 to 2000. The partition lines and arrows are drawn by hand.

composition (Fig. 3). Station Nw2 north of the Rhine discharge, for instance, was characterized by high nutrient concentrations (DIN, DIP, Si) and a high temperature (Fig. 3a). Wa2, Gr6, and MdN had a high SPM and K_d , in contrast to the most northern station Ts4 with a high salinity (Fig. 3b). Based on phytoplankton composition the main difference in locations was related to PCO axis 1 (84% of total variation; 8% by axis 2) with apparent low species abundances at Wa2 and Gr6 (southern stations) and higher abundances to the north (Ts4, MdN; Fig. 3, c and d).

When yearly averaged data were plotted in PCO diagrams, a remarkable partitioning in both abiotic and phytoplankton data became apparent (Fig. 4). In the abiotic data, one partition is between years with contrasting salinities (group 1 and 2; Fig. 4a) as salinity is the main vector perpendicular to the partition line (Fig. 4b). For instance, the large distance between 1995 and 1996 indicates a large interannual variability. The difference between both “inter-annual” low and high salinity groups of years was significant (Table 3).

A second partition is in two groups of consecutive years: 1991–1998 (group 3) and 1999–2005 (group

4) with a shift occurring from 1998 to 1999 (Fig. 4a). Influential abiotic variables in separating groups 3 and 4 were DIP, pH, and SPM: all three were relatively high before and including 1998 and relatively low thereafter (Fig. 4b). The interannual and the shift groups were, according to a PERM-DISP test, not different in their within-group dispersion. The difference between both “shift”-groups of years was significant (Table 3).

The phytoplankton also showed two partitions (Fig. 4c). Group 1 and 2 are separated according to interannual differences and group 3 and 4 by a long-term shift from 1999 to 2000. The interannual differences are characterized by an increase in summer and autumn diatoms such as *Rhizosolenia*

TABLE 3. PERMANOVA of the abiotic and phytoplankton data partitioned in two groups according to interannual differences and to a long-term shift (see Fig. 5).

Source	df	Abiotics		Phytoplankton	
		Pseudo-F	P	Pseudo-F	P
Interannual	14	7.1	<0.001	3.0	<0.001
Shift	14	5.5	<0.005	2.8	<0.005

delicatula (Fig. 4d). The main difference between the two long-term phytoplankton groups appeared to be related to a decrease in the abundance of *Asterionella glacialis* and increases in *Phaeocystis globosa* and two winter diatoms (*Paralia marina* and *Thalassionema nitzschioides*; Fig. 4d). The interannual and the shift groups were, according to a PERMDISP test, not different in their within-group dispersion. The difference between the “inter-annual” and the long-term “shift” phytoplankton groups was significant (Table 3).

Time-series diagrams of the yearly averaged abiotic data clearly showed interannual differences (Fig. 5). For instance, 1996 had a low average temperature that was accompanied with high salinity and relatively low DIN, DIP, and Si concentrations (Fig. 5, a–e), in accordance with the PCO ordination (Fig. 4, a and b). An apparent 7-year (1996–2002) increase

in temperature coincided with a decrease in salinity in the same period (Fig. 5, a and b). DIP decreased by 50% from 1991 to 2005 (Fig. 5d). SPM dropped sharply from 1998 to 1999 and decreased steadily from 2000 onwards (Fig. 5f). pH decreased by 0.2 units from 1995 to 2005 (Fig. 5g). As expected from equation 1 the irradiance attenuation coefficient covaried with SPM (Fig. 5h).

The effect of salinity on a number of variables was examined in linear regression analyses. Temperature, DIN, and Si were significantly correlated to salinity with DIP and SPM as exceptions (Fig. 6, a–e). Salinity itself was highly correlated to Rhine discharge (Fig. 6f). The irradiance attenuation coefficient was correlated to salinity (Pearson $r^2 = 0.40$, $P < 0.05$), partly because of autocorrelation (Eq. 1). pH was not correlated to salinity; it was best

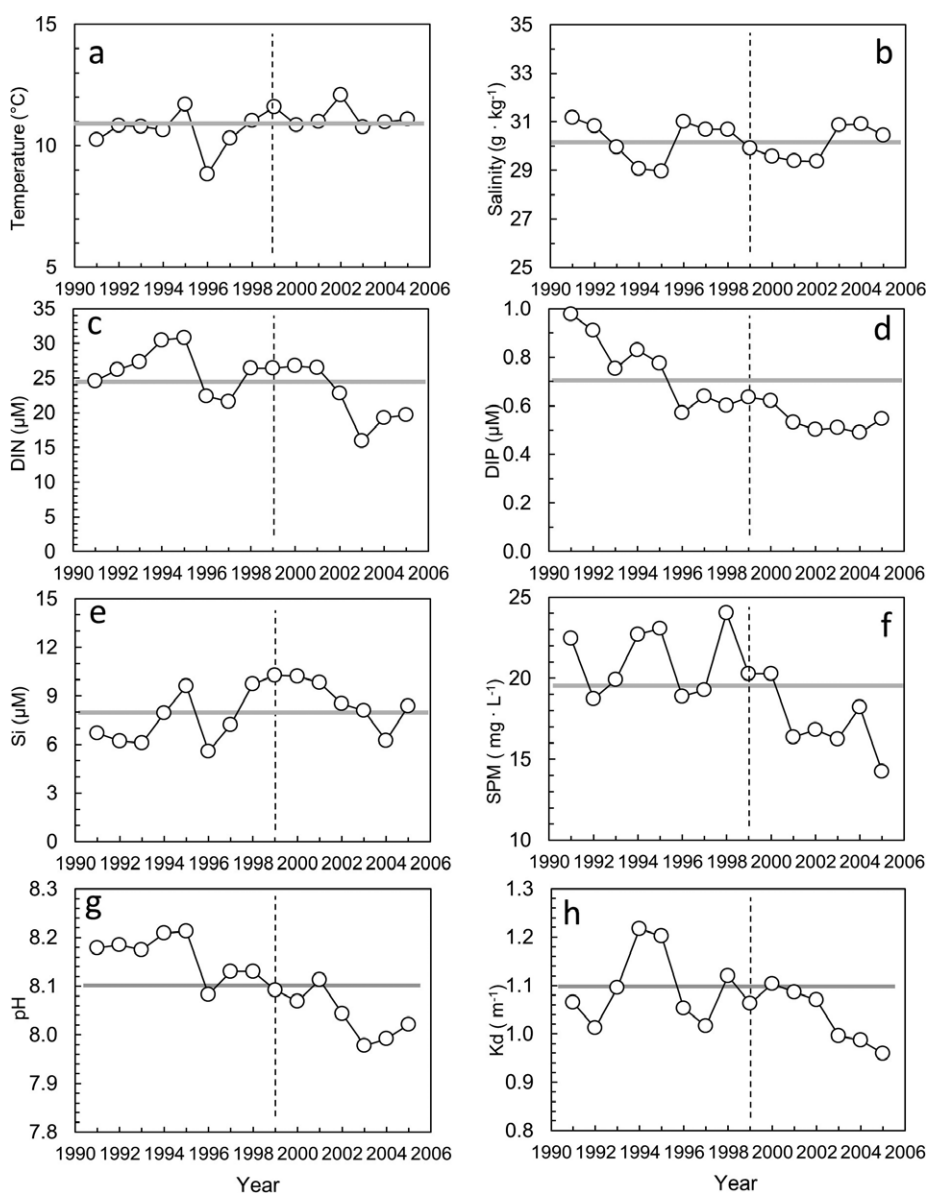


FIG. 5. Development of yearly averaged abiotic variables along the Dutch coast. (a) Temperature, (b) salinity, (c) dissolved inorganic nitrogen, (d) dissolved inorganic phosphorus, (e) silicate, (f) suspended matter, (g) pH, (h) irradiance attenuation coefficient (K_d). The vertical line indicates the first year after the shift in the multivariate abiotic ordination. The horizontal line is the 15 year average.

correlated with DIP (Pearson $r^2 = 0.78$, $P < 0.001$, not shown).

The absence of correlation between SPM and salinity instigated a further investigation of the cause of the 1998–1999 decrease in SPM (Fig. 5f) because of the considerable influence SPM has on irradiance attenuation (Eq. 1) and underwater light climate (Eq. 2). A prime suspect of the SPM decrease is a change in wind speed because winds strongly influence sediment resuspension in the Dutch coastal zone (Blauw et al. 2006). Although variable, the average wind speeds along the Dutch coast were high at the beginning of the 1990s and low after 2000 (Fig. 7a). Because wind speeds over the North Sea are related to the NAO winter index (Siegismund and Schrum 2001) the annual averaged Dutch coastal wind speeds were compared to the annual NAO index (Fig. 7b). Wind speed and

NAO index had a comparable pattern in time with high values in the early 90s and ~1999, followed by a decline.

The comparable patterns in wind speed and annual NAO index is reflected in a significant correlation (Fig. 8a). As expected, SPM is correlated with wind speed (Fig. 8b). The effect of a decrease in wind speed is an increase in water column irradiance (Fig. 8c). Hence, the increase in daily irradiance since 1999 is at least partly an effect of reduced wind speeds although there is no direct correlation with the NAO index (Fig. 8d).

Interannual variability was also present in the phytoplankton time-series diagrams of six selected species with a different seasonal abundance (Fig. 9). In 1995, a year with low salinity, relative peaks in abundance occurred in summer and autumn diatoms (Fig. 9, d–f). The long-term shift in the phytoplankton ordination

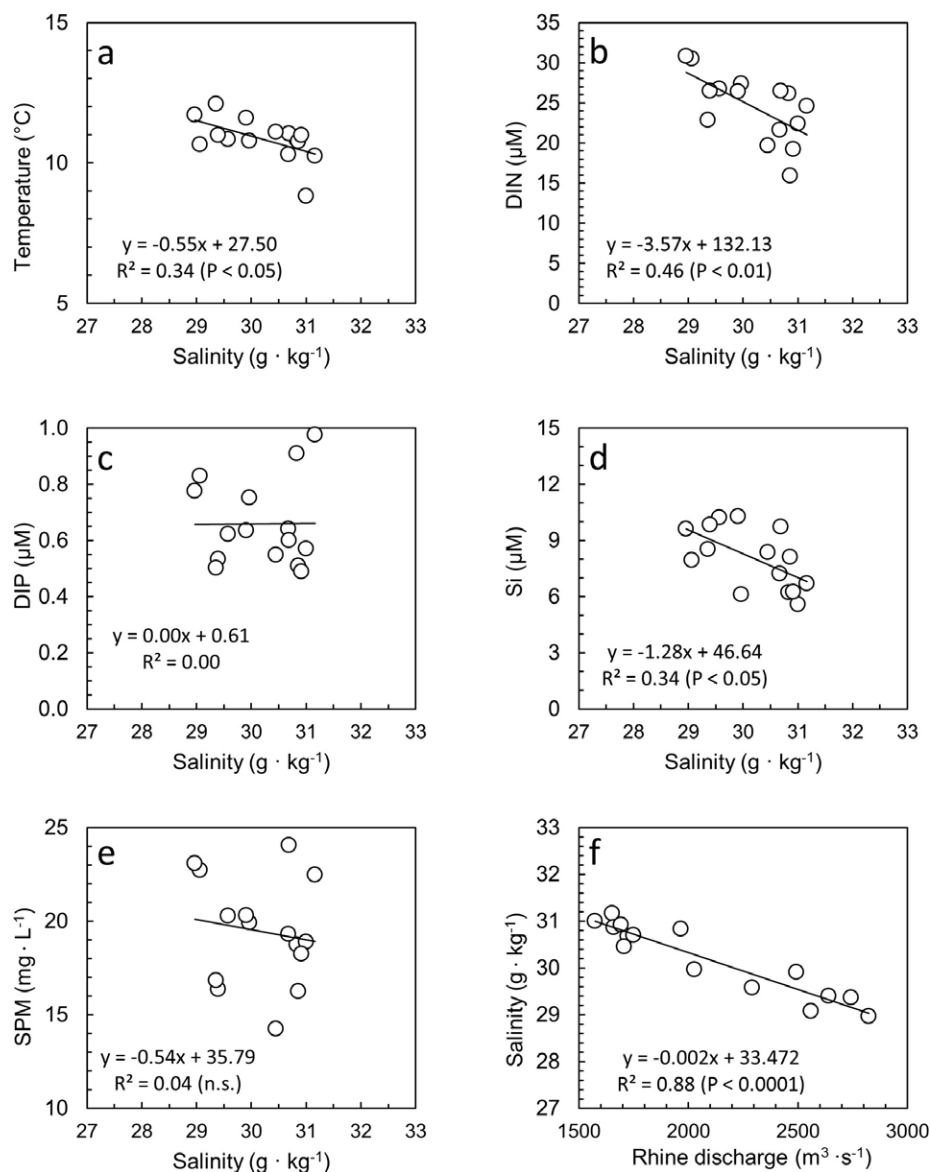


FIG. 6. Correlations of annual averaged temperature (a), DIN (b), DIP (c), Si (d), and SPM (e) with coastal zone salinity, which itself is strongly correlated with Rhine discharge (f).

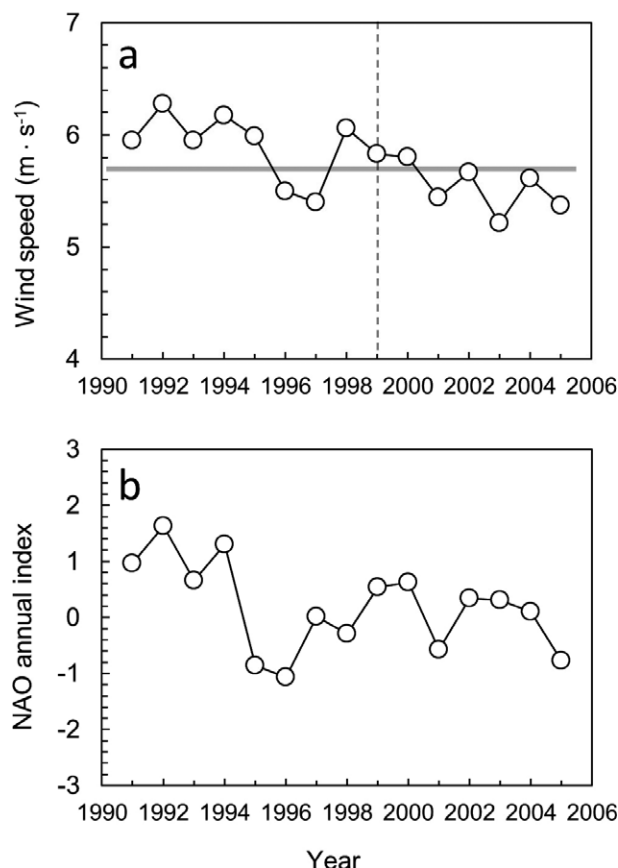


FIG. 7. Development of yearly averaged wind speed (a) in the Dutch coastal zone and annual NAO index (b). The vertical line in a indicates the first year after the shift in the multivariate abiotic ordination (Fig. 4a). The horizontal is the 15 year average. The wind speeds were relatively high in the early 1990s and relatively low after 2000. A comparable pattern was followed by the annual NAO index.

was also visible but not as straightforward as in the abiotic data. After 1998, the two winter diatoms *Thalassionema nitzschoides* and *Paralia marina* increased in abundance, that is, in the same year as the abiotic shift took place (Fig. 9, a and b). *Phaeocystis globosa* peaked in the cold 1996 and increased after 1999 with a remarkable minimum in 2002 (Fig. 9c). The summer diatoms (*Rhizosolenia delicatula*, *Odontella sinensis*) peaked again in 2001 as did *P. marina* and *P. globosa*, then decreased in abundance (Fig. 9, d and e). The abundance of the diatoms *Rhizosolenia setigera*, *Rhizosolenia shrubsolei*, and *Torodinium robustum* were variable while a slight decrease took place in *Asterionella glacialis* since 1997 (Fig. S1 in the Supporting Information).

The relation between interannual phytoplankton variability and salinity was investigated by regressions using Rhine discharge which is a good predictor for salinity (Fig. 6f). The winter diatoms and *Phaeocystis globosa* did not correlate with Rhine discharge (Fig. 10, a-c), nor did the spring species *Asterionella glacialis* and *Torodinium robustum* or the spring-summer diatoms *Rhizosolenia setigera* and *R. shrubsolei*

(not shown). On the other hand, four summer to autumn diatoms did significantly correlate with Rhine discharge (Fig. 10, d-f).

The increase in *Phaeocystis globosa* (Fig. 9c), a presumed harmful algal bloom species historically related to eutrophication (Cadée and Hegeman 1986), was remarkable given the continuous decrease in DIP (Fig. 5d) and was examined in more detail by linear regression analyses for each station separately (Fig. 11). The increase in abundance took place at all stations except MdN and was not significant at Wa2 (Fig. 11, a and d). Excluding MdN, the average *P. globosa* increase from 1991 to 2005 was highly significant (Fig. 11f). The null hypothesis that excluding MdN from the calculation of the similarity matrices used for the PCO ordinations would lead to no relation between the full and reduced matrices was rejected (RELATE abiotic $\rho = 0.94$, $P < 0.001$, phytoplankton $\rho = 0.84$, $P < 0.001$). In other words, the exclusion of MdN does not lead to different conclusions on interannual and long-term variability.

Water column daily irradiance is an important factor in the development of *Phaeocystis globosa* blooms (Peperzak 1993, 1998). Therefore, the relation between *P. globosa* abundance and the factors that influence daily irradiance were examined in more detail. *P. globosa* abundance was negatively correlated to wind speed and SPM, and positively, but not significantly, to daily irradiance (Fig. 12, a-c). A lower-negative-NAO index is related to a higher *P. globosa* abundance (Fig. 12d). The negative correlation between NAO and *P. globosa* abundance of $r^2 = 0.46$ (Fig. 12d) improved to $r^2 = 0.68$ ($P < 0.0005$) after omitting 1995, a year with a low NAO but high wind speeds (Fig. 7a).

Wind was the single best predictor of phytoplankton composition in the DistLM models (Table 4). Out of six physical variables, four explained nearly 50% of the variation ($r^2 = 0.47$). Adding Si, the best out of four chemical variables increased this only slightly ($r^2 = 0.52$). Visualization of this 4 + 1 model (Fig. 13) yielded a phytoplankton ordination that included both interannual variation (group 1 vs. group 2) and the long-term shift (group 3 vs. group 4), although this shift now took place from 1998 to 1999, as it did in the PCO for abiotic data (Fig. 4a). In the PCO for phytoplankton, the shift took place from 1999 to 2000 (Fig. 4c). The ordination of all other years strongly resembled the original phytoplankton PCO ordination in Figure 4c.

DISCUSSION

The relatively short 1991–2005 data set captured both interannual and long-term abiotic variability of the Dutch coastal zone. Temperature and salinity were variable, although a 7 year periodicity was apparent in the salinity data. A 7 year salinity periodicity has also been noted in the German Bight and was related to a 7.7 year frequency in the NAO

FIG. 8. Correlations between wind speed and annual NAO index (a), suspended matter concentration and wind speed (b), mean water column daily irradiance and wind speed (c) and daily irradiance and annual NAO index (d). The NAO index is significantly correlated to wind speed (a), which itself is significantly correlated to suspended matter concentration (b) and irradiance (c). The NAO index is not correlated directly to irradiance (d).

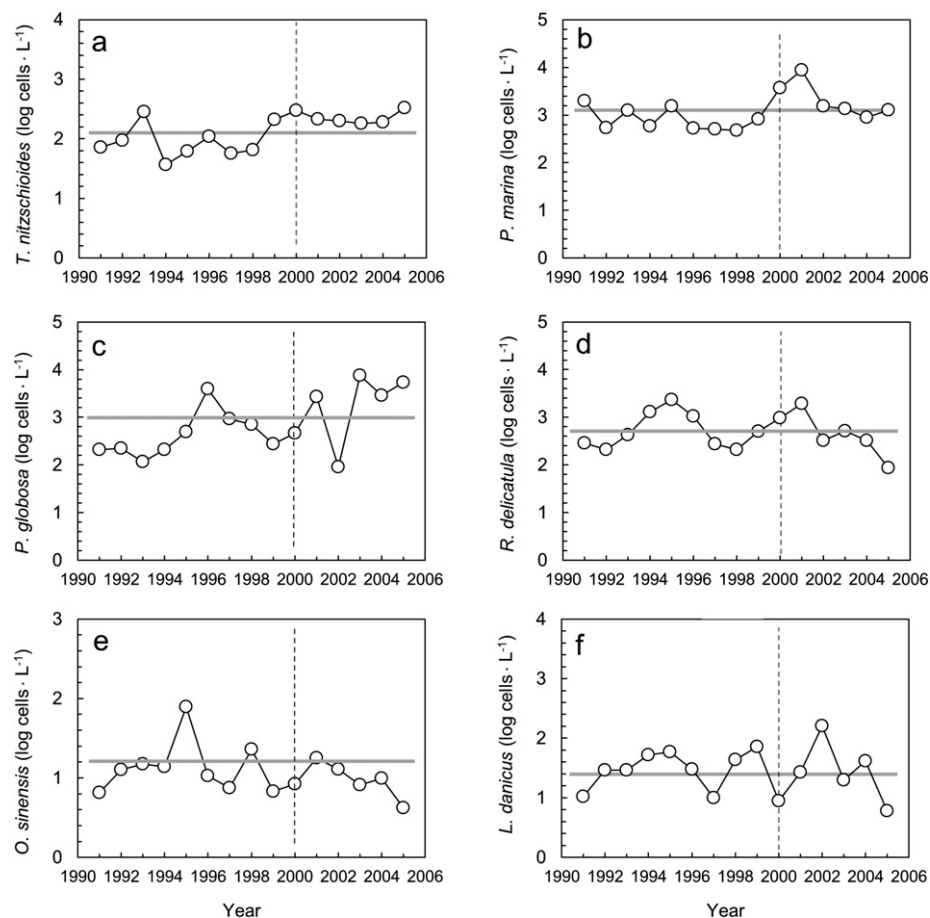
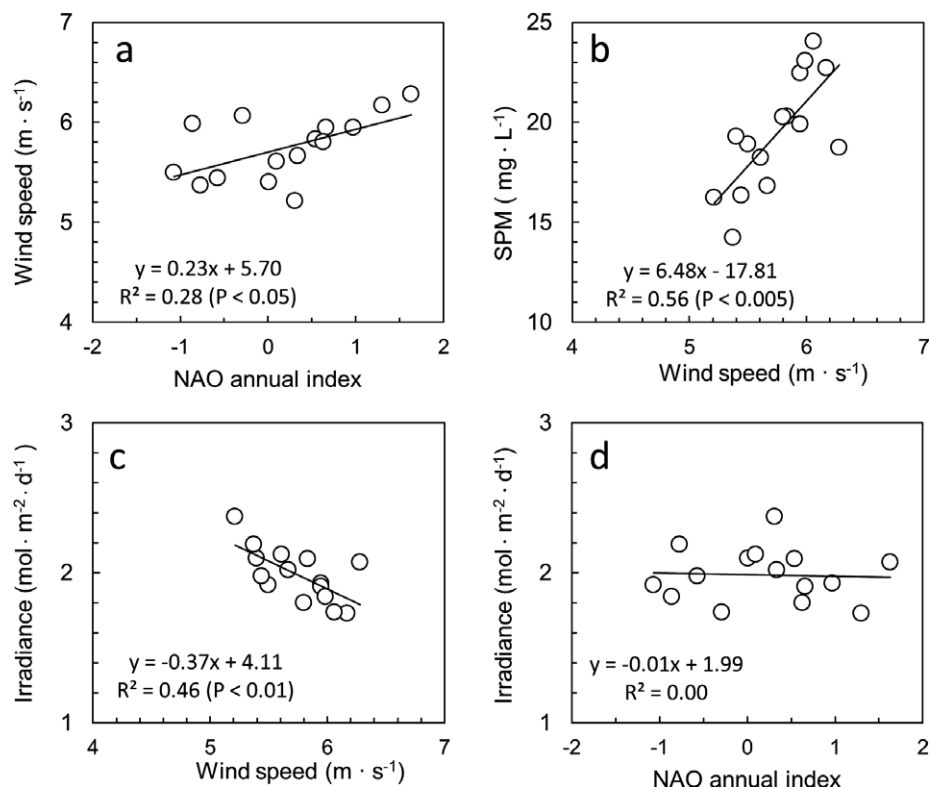


FIG. 9. Development of phytoplankton species abundances in the Dutch coastal zone. Winter to autumn species were selected. (a) *Thalassionema nitzschoides* (winter), (b) *Paralia marina* (winter), (c) *Phaeocystis globosa* (spring), (d) *Rhizosolenia delicatula* (summer), (e) *Odontella sinensis* (summer), (f) *Leptocylindrus danicus* (autumn). The vertical line indicates the first year of the phytoplankton shift. The horizontal line is the 15 year average.

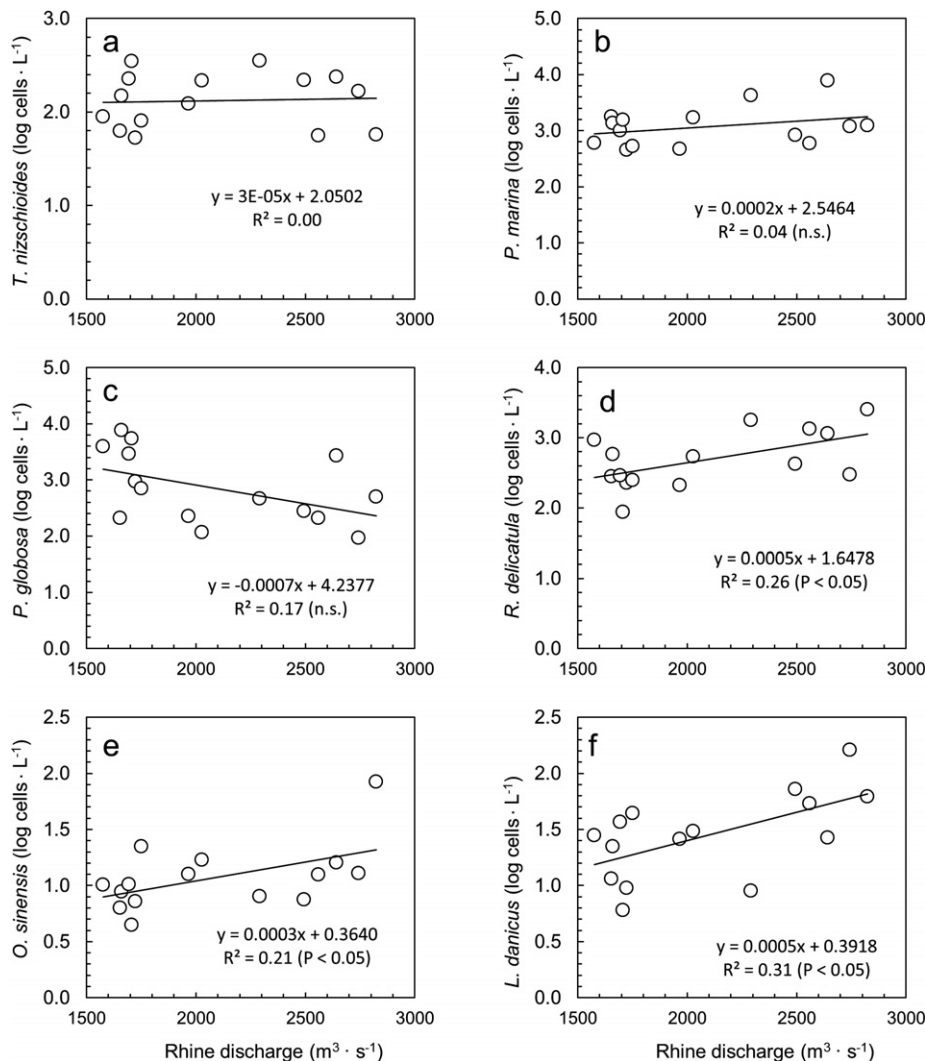


FIG. 10. Correlations between phytoplankton abundance and Rhine discharge. Winter to autumn species were selected. (a) *Thalassionema nitzschioides* (winter), (b) *Paralia marina* (winter), (c) *Phaeocystis globosa* (spring), (d) *Rhizosolenia delicatula* (summer), (e) *Odontella sinensis* (summer), (f) *Leptocylindrus danicus* (autumn).

index (Sundermann et al. 1996). No correlation was, however, found between the salinity in the Dutch coastal zone and the annual NAO index (results not shown). Nutrient concentrations declined from 1991 to 1996 (DIP), declined after 2000 (DIN), or covaried with salinity (Si). Remarkable is the change in pH at -0.02 units per year from 1995 to 2005, which is a factor 10 higher than ocean model calculations for the 21st-century shown as the result of increased atmospheric CO₂ (Orr et al. 2005). Although there is no apparent causation, there is a high correlation of pH and DIP.

The Dutch coastal zone is not a homogenous water mass. PCO ordinations showed that the most northern station (Ts4) is a relative abiotic outlier: it has a relatively high salinity because it is furthest away from a freshwater source. Station MdN is a phytoplankton outlier, probably because it is situated in a zone where the North Sea and the Wadden Sea are mixed (van Aken 2008a,b). Time-series diagrams of *Phaeocystis globosa*, one of the most abundant species in the Dutch coastal zone, not only emphasized the

differences between the locations but also the uniqueness of station MdN in this data set.

Interannual abiotic changes before and after 1998 were related to salinity and the correlated water temperature and nitrogen and silicate concentrations. In the abiotic long-term regime shift from 1998 to 1999 on the other hand, the decrease in DIP, pH, and in SPM were major factors. While DIP and pH declined after 2000–2001, a factor of two decrease in SPM took place between 1998 and 2005 that led to a strong reduction in the irradiance attenuation coefficient. The strong decline in SPM pointed to an environmental factor external to the initial aquatic abiotic data set.

SPM concentrations in the Dutch coastal zone are highly influenced by wind-induced turbulence. A 2-fold increase in the annual fluxes of suspended solids in Dutch coastal waters in the 1980s has been attributed to a rise in strong winds (Van Alphen 1990). Strong winds cause sediment resuspension (Van Alphen 1990, Witbaard et al. 2005, Blauw et al. 2006). Wind speeds over the North Sea

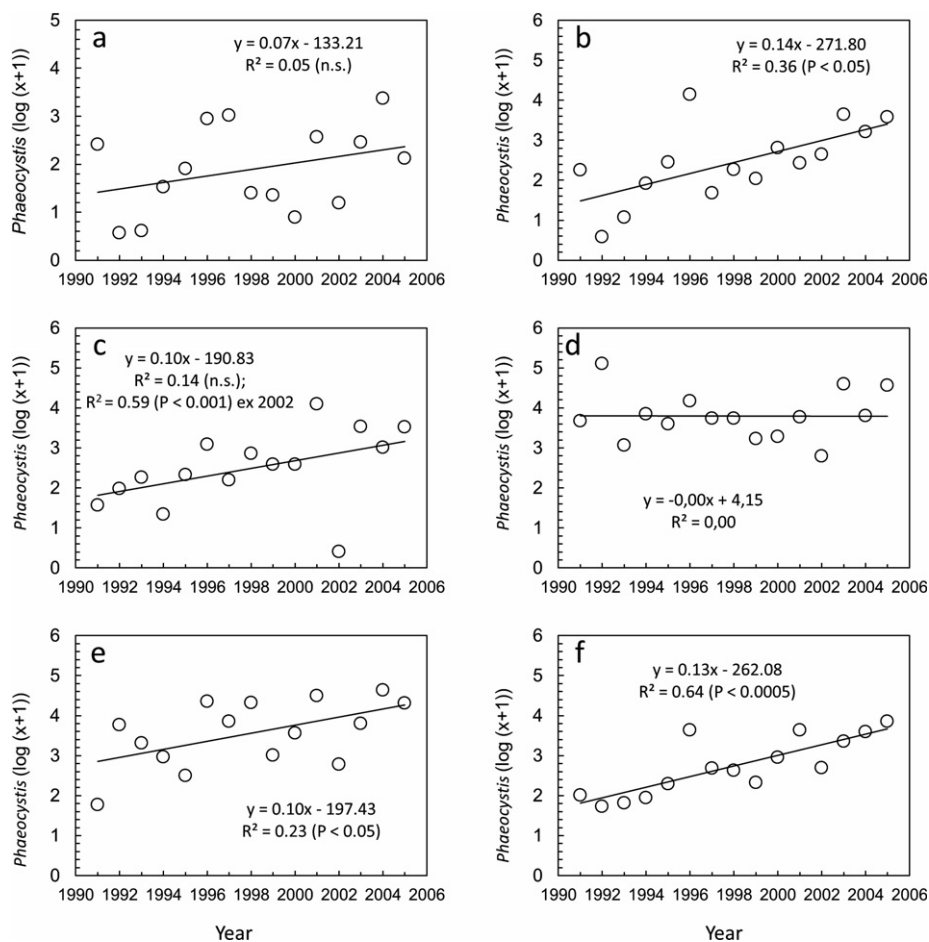


FIG. 11. Development of yearly averaged *Phaeocystis* in the Dutch coastal zone. (a) Wa2, (b) Gr6, (c) Nw2, (d) MdN, (e) Ts4, and (f). All stations averaged with MdN excepted. Lines are the linear regression lines. With the exception of MdN, all stations show an increase in *Phaeocystis* abundance. Peaks occurred in 1996 and 2001.

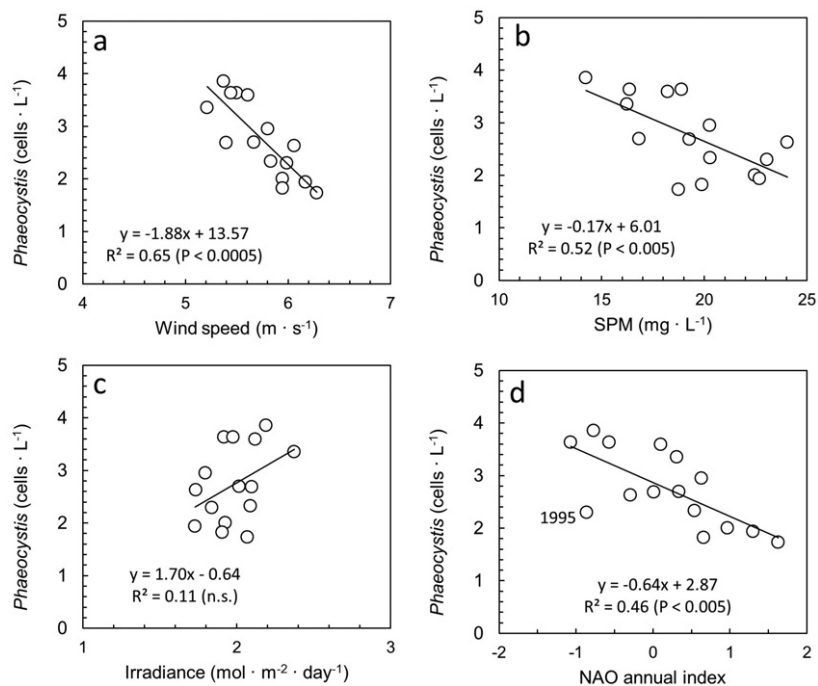


FIG. 12. Correlations between mean *Phaeocystis* abundance and wind speed (a), suspended matter concentration (b), Daily water column irradiance (c) and the annual NAO index (d). Location MdN was not included in the averages of *Phaeocystis* and SPM. The correlation in d improved to $r^2 = 0.68$ ($P < 0.0005$) after omitting 1995, a year with a low NAO but high wind speeds.

TABLE 4. distLM analyses of abiotic variables explaining the multivariate phytoplankton composition. Included in the analysis were six physical (T, SPM, Em, NAO, wind, and Rhine) and four chemical variables (pH, DIN, DIP, Si). Physics (four variables) is the best solution from the six physical variables. Out of four, Si is the best chemical variable to add to the four physical variables.

Number of variables		R^2	AIC
1	Wind	0.18	63.7
2	SPM+Rhine	0.32	62.9
3	SPM+Rhine+NAO	0.42	62.5
4	Rhine+NAO+pH+DIP	0.50	62.2
4 (Physics)	Rhine+NAO+SPM+T	0.47	63.0
5	Rhine+NAO+pH+DIP+SPM	0.58	61.7
5	Physics+1 chemical variable (Si)	0.52	63.6
11	All	0.82	59.3

increased from the late 1950s till the 1990s, with an increase in strong wind events since the mid-1980s in February and March, that is, during early spring (Siegismund and Schrum 2001). This long-term increase in wind speeds was correlated to the winter NAO index (Siegismund and Schrum 2001). The annual averaged wind speed in the Dutch coastal zone declined consistently after 1998 and was also significantly correlated to the annual NAO index. A correlation between winter NAO index and wind stress was also found for the whole coastal North Sea (McQuatters-Gollop and Vermaat 2011). Thus, a large-scale meteorological index as the NAO has a profound effect on wind speeds along the Dutch coast that, in turn, influence SPM and underwater irradiance.

Sudden changes from one stable ecosystem state to another stable state are termed regime shifts (Weijerman et al. 2005). A well-known example is the shift from anchovy to sardine regimes in the Humboldt Current that is related to the El Niño

Southern Oscillation (Alheit and Niquen 2004). Furthermore, the effect of changes in oceanic weather patterns is not restricted to marine waters. The annual biomass of freshwater zooplankton in UK lakes is also influenced by the NAO (George and Taylor 1995, Taylor and Stephens 1998). One regime shift that took place during the period 1982–1988 in the North Sea had the winter NAO index as a pivotal actor with an effect on both sea surface temperature, wind speed, and wind direction (Beaugrand 2004). A first regime-shift in the North and Wadden Sea took place in 1979, while a second shift in this region was identified slightly later in 1989 (Weijerman et al. 2005). A third shift in 1998 was deemed possible but was not clearly discernible in the principal component scores in the PCA analysis used (Weijerman et al. 2005). Using Rodionov's sequential *t*-test on the principal component scores from PCA analysis, shifts in hydroclimatic variables in coastal and open North Seawaters were detected in 1977, 1989, 1997, and 2001 (McQuatters-Gollop and Vermaat 2011). Therefore, the year of the regime-shift appears to be variable as it depends on the statistical technique used (Beaugrand 2004).

An additional factor that might blur the exact timing of regime-shifts, in this case in the North and Wadden Sea, may be the use of highly complex and various abiotic and ecological data sets (Weijerman et al. 2005, McQuatters-Gollop and Vermaat 2011). Furthermore, the use of compound categories, such as “total copepods” or “diatom abundance”, that contain many different species that may respond differently to abiotic change may obscure shifts (Beaugrand 2004). In the present PCO and PERMANOVA analysis, compact but complex sets of abiotic and phytoplankton species data that differed from previous studies were used which may explain the location of the shift in 1999–2000, in between those in 1997 and 2001 (McQuatters-Gollop and Vermaat 2011).

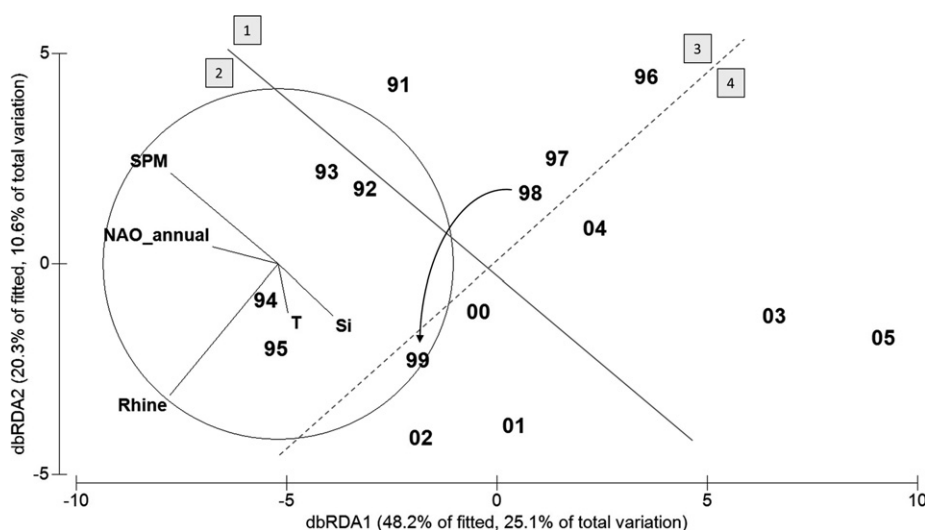


FIG. 13. Distance-based redundancy analysis ordination of the fitted phytoplankton composition based on a model of one chemical and four physical predictor variables. The numbers designate years (1991–2005). The gray and the dashed partition lines are drawn by hand. According to this model group 1 and 2 are separated according to interannual differences and group 3 and 4 by a long-term shift from 1998 to 1999.

The results of the present study identified abiotic regime shifts in 1999 and 2000 for the Dutch coastal zone are close to previously reported North Sea shifts from 1997 to 2001 (Weijerman et al. 2005, McQuatters-Gollop and Vermaat 2011). In addition, by using NMS analysis, concomitant and significant changes in 2000 and 2001 have been observed in the Dutch coastal zone in the zoobenthos community (R. Witbaard, pers. comm.). Furthermore, a significant shift in the abundance of five zooplankton species was measured by the CPR in standard area D1 off the Dutch coast (Fig. 1) from 2001 to 2002 (L. Peperzak, unpub. data). It appears that the community structures of phytoplankton, zooplankton, and zoobenthos in the southern North Sea all changed around the turn of the century.

Phytoplankton growth in the Dutch coastal zone is first P- then Si-limited (Peeters and Peperzak 1990, Peperzak et al. 1998). It is, therefore, not surprising that interannual variability related to salinity and silicate affected summer to autumn diatoms. The start of the spring bloom, when nutrients are still in excess, is controlled by light (Peeters et al. 1991, Peperzak et al. 1998). McQuatters-Gollop et al. (2007) examined the effect of the 1980s regime-shift for chlorophyll-*a* concentrations in the open and coastal North Sea by linear regression analysis. Coastal chlorophyll-*a* was best predicted by winter Secchi depth and sea surface temperature, and it was suggested that light-limited coastal phytoplankton could more effectively utilize the lowered concentrations of nutrients due to less turbid water (McQuatters-Gollop et al. 2007). This explanation may also be applicable to the increase in several winter-spring phytoplankton species as a result of decreasing SPM in the Dutch coastal zone after 1998. In particular, *Phaeocystis globosa* abundance increased after the decrease in wind speed and SPM and an increase in water column daily irradiance, despite the long-term decreases in DIN and DIP concentrations. At Nw2 the average start of the *Phaeocystis globosa* spring bloom moved forward from April 26 (1994–1999) to March 23 (2001, 2003–2005; L. Peperzak, unpublished data). This chain of events from wind speed to *Phaeocystis globosa* abundance underlies this species correlation with the NAO index. In contrast, Breton et al. 2006 only found an indirect effect of the NAO on the 1988–2001 diatom/*Phaeocystis globosa* blooms in the Belgian coastal zone south of monitoring station Wa2 (Fig. 1), and through Westerschelde discharge combined with wind speed and direction. This discrepancy may reflect different geographies, study years, and statistical techniques used. Clearly, a uniform analysis of combined international datasets is needed to resolve this seeming disagreement.

The phytoplankton composition from 1991 to 2005 could adequately be modeled with five variables, of which three relate strongly to interannual

variability (Rhine discharge), as well as the 1999 shift (SPM, Si). In addition, the strong correlations between *Phaeocystis globosa*, a presumed harmful algal species, and a variable such as the NAO index or wind speed offer a possibility to better model the long-term annual abundance of *Phaeocystis globosa*, hitherto not possible for the Dutch coastal zone (Blauw et al. 2006). As a first step in modeling the abundance of other species, such as the diatoms, regression models comparable as presented here should be investigated. For instance, summer diatom abundance is correlated to Rhine discharge and might well be better correlated to the concentrations of specific nutrients.

The present investigation used data from the Dutch coastal zone, a shallow and turbulent region of which it was assumed it had an along the coast homogeneous distribution of abiotic and phytoplankton variables. This assumption is proven wrong: monitoring stations are different in abiotic and phytoplankton variables and large interannual variability and long-term shifts occur. To understand phytoplankton variability and in order to build species-specific phytoplankton models, for instance predictive models for specific harmful species, these should also encompass station-specific abiotic characteristics in order to capture geographic variability. The large spatial gradients in salinity, nutrients, turbulence, and in water column irradiance perpendicular to the Dutch coast (Gieskes and Kraay 1975, van Bennekom and Wetsteijn 1990, Peeters et al. 1991, Peperzak 1993), as well as the high temporal variability due to interannual and long-term abiotic shifts will be helpful in the process of identifying and quantification of the abiotic characteristics that affect the abundance of specific phytoplankton species.

We thank Rijkswaterstaat (Waterbase helpdesk and M. Latuhihin) for providing help on data retrieval. Dr. K. Timmermans (NIOZ) critically read the manuscript. We also thank two anonymous reviewers for their help in improving the manuscript. We declare there are no conflicts of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Abiotic drivers of interannual phytoplankton variability and a 1999–2000 regime shift in the North Sea examined by multivariate statistics. Development of phytoplankton species abundances in the Dutch coastal zone. (a) *Rhizosolenia setigera*, (b) *R. shrubsolei*, (c) *Torodinium robustum*, (d) *Asterionella glacialis*. The vertical line indicates the first year of the phytoplankton shift. The horizontal line is the 15 year average.