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Recent patterns in potential phytoplankton limitation along the Northwest European continental coast

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ABSTRACT

The European coastal zone is characterized by high anthropogenic riverine nutrient loads, and turbid waters along the continental North Sea coastal stretch. Riverine nutrient inputs (N and P) have increased since the 1950's and have decreased again since the mid 1980's. Using the approach of Cloern (Cloern, J.E., 1999, *Aquatic Ecology* 33, 3–16), we analyzed potential limitation patterns of light and nutrients (DIN, PO₄, Si) for seven long-term monitoring stations along the North Sea coast. As available, data from 1990 until 2005 were analyzed. Underwater irradiance was the dominant factor potentially limiting phytoplankton growth. Seasonal limitation patterns strongly differed between the investigated sites. Si limitation was the most common among the stations followed by PO₄ limitation. Only one station with optimum light conditions (northern Wadden Sea) resulted a potential DIN limitation. An increase in nutrient limitation, or co-limitation of light and nutrients, was observed off the Dutch coast (DIN and PO₄), and in the German Bight near Helgoland (DIN, PO₄, Si) within the period from 1990 until 2005. However, we observed no clear effects of nutrient reduction measures in shallow areas of the Wadden Sea during the period studied. We conclude that long-term nutrient limitation patterns are consistent and site dependent, and strongly linked to the local hydrography and light conditions of the water column.

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1. Introduction

Eutrophication along the European North Sea coast started mainly in the 1950's as increasing amounts of fertilizer were used in modern agriculture and population density increased (Nienhuis, 1992; Lotze et al., 2005; Billen et al., 2005). In addition, canalization networks were extended, thus releasing large amounts of inorganic nutrients into the river system (Van Bennekom and Wetsteijn, 1990). Compared to 19th century levels, the riverine nitrogen loads into the North Sea and the Wadden Sea increased at least eight-fold (Van Bennekom and Wetsteijn, 1990; Nienhuis, 1992; Van Beusekom, 2005). Since the mid-1980's nutrient loads of the dominating rivers, like Rhine, Scheldt, Maas, Weser, and Elbe, decreased as a result of waste water treatment, a ban on P-containing detergents and other European management strategies (e.g. De Jonge et al., 1996; Van Beusekom et al., 2005; Carstensen et al., 2006; Soetart et al., 2006).

Possible consequences of increased riverine nutrient loads include increased blooms of the Haptophyceae *Phaeocystis* (Lancelot et al., 1987), an increase in primary production (e.g. Cadée and Hegeman, 2002), increased green macro-algae in the Wadden Sea (Reise and Siebert, 1994), and hypoxic areas developed in the German Bight (Gerlach et al., 1985; Gerlach, 1990). An attempt has been made to relate long-term fluctuations of *Phaeocystis* blooms in the Southern Bight of the North Sea to changes either in climate (Owens et al., 1989) or to anthropogenic nitrogen and phosphorus loads (Cadée and Hegeman, 1991); however the outcome is unclear. These hypotheses were recently reconciled by Breton et al. (2006) who showed that in near shore waters like the Belgian coastal zone (BCZ), large-scale hydrographic and meteorological conditions interact with the local influence of riverine nutrient loads.

Phytoplankton may respond to the increased riverine nutrient loads by an increase in primary production and chlorophyll-*a* (Chl-*a*) concentrations (e.g. Cadée and Hegeman, 2002). The authors reported low potential pelagic primary production levels in the Marsdiep area: about 150 g C m⁻² y⁻¹ for the period 1964–1975, increasing to 440 g C m⁻² y⁻¹ in 1994, and decreasing afterwards to values between 200 and 250 g C m⁻² y⁻¹ in 2000. Chl-*a* values remained on a similar level from

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the mid 1990's onward (Philippart et al., 2007). The TN:TP ratio at the start of the spring bloom in the Marsdiep tidal inlet has increased from about TN:TP=15±2 in the mid 1980's to TN:TP=21±3; a change in species dominance with less diatoms and increased flagellates was also observed (Cadée and Hegeman, 2002; Philippart et al., 2007). The reduction in riverine nutrient loads may have changed the food web in the western Dutch Wadden Sea, with possible consequences for the standing stock of benthic consumers such as mussels or top predators like birds and fishes (Philippart et al., 2007).

The most recent legislation for improving the ecological status in European coastal waters is the European Union Water Framework Directive (Anon., 2000). The difficulties in assessing the impact of the EU-directives on coastal ecosystems are discussed, e.g. by De Jong (2006) and Colijn and Garthe (2005). They conclude that future long-term observations and experiments are needed to understand the long-term ecosystem changes due to human impacts including the effects of countermeasures.

Phytoplankton is at the basis of marine food webs; its growth is controlled by light and by nutrient availability. We investigated the present pattern of potential phytoplankton growth limitation along the North Sea coastal zone during the past 15 years (1990–2005) to test long-term effects of nutrient reduction measures. We used the model proposed by Cloern (1999) to assess spatial and temporal patterns of potential phytoplankton growth limitation by light and nutrients (DIN, PO₄, Si), at seven long-term monitoring stations along the North Sea coastal zone.

2. Methods

2.1. Study area

Our study includes data sets of seven monitoring stations along the European coast from the Belgian coast to the northern Wadden Sea (Fig. 1; Table 1). At all sites, the water column is homogeneously mixed. Table 1 summarizes the hydrographic characteristics of these stations.

2.2. Data sets on nutrients, irradiance, and turbidity

For all analyses, we used hourly irradiance data from the weather station (Deutsche Wetter Dienst) on the Island of Sylt. Although differences occur along the coastline, they are relatively minor over this small range in latitude (51°N–55°N). Dissolved inorganic nutrient concentrations (DIN [NO₃+NO₂+NH₄], PO₄, Si), chlorophyll-a concentrations, and Secchi depths (or suspended matter concentrations) were taken from time series measurements at the respective sampling locations. Nutrients were analyzed with standard wet chemical techniques. All nutrient and chlorophyll-a data are based on surface samples. No intercalibration has taken place between the institutes, thus it is not possible to compare the quality of the nutrient and chlorophyll measurements at the selected positions.

2.3. Calculation of growth rate in relation to light and nutrients

Cloern (1999) developed a simple model based on Liebig's Law of the Minimum to investigate the dependency of phytoplankton growth rates on underwater irradiance and nutrient concentrations. His model can be used to compare the sensitivity of estuaries and shelf seas to changes in the potential limitation due to nutrients or light availability.

Cloern empirically developed resource limitation maps as contour plots of phytoplankton growth rate sensitivity to water column irradiance and nutrients. R is the ratio of mean water column irradiance and nutrient concentration where $R > 10$ indicates strong potential light limitation and $R < 0.1$ indicates strong potential nutrient limitation. Values between 0.1 and 10 are indicative of a potential co-limitation. Phytoplankton growth limitation by two nutrients (e.g. DIN and PO₄) cannot directly be compared by this model, but the relative nutrient limitation against light can be used in a comparative way.

We used Cloern's model to calculate growth rate sensitivity to light and nutrients at the seven sites along the European continental coast on a monthly basis (if data were available) between 1990 and 2005 (Table 1). As suggested by Cloern, concentrations of DIN, PO₄, and Si were

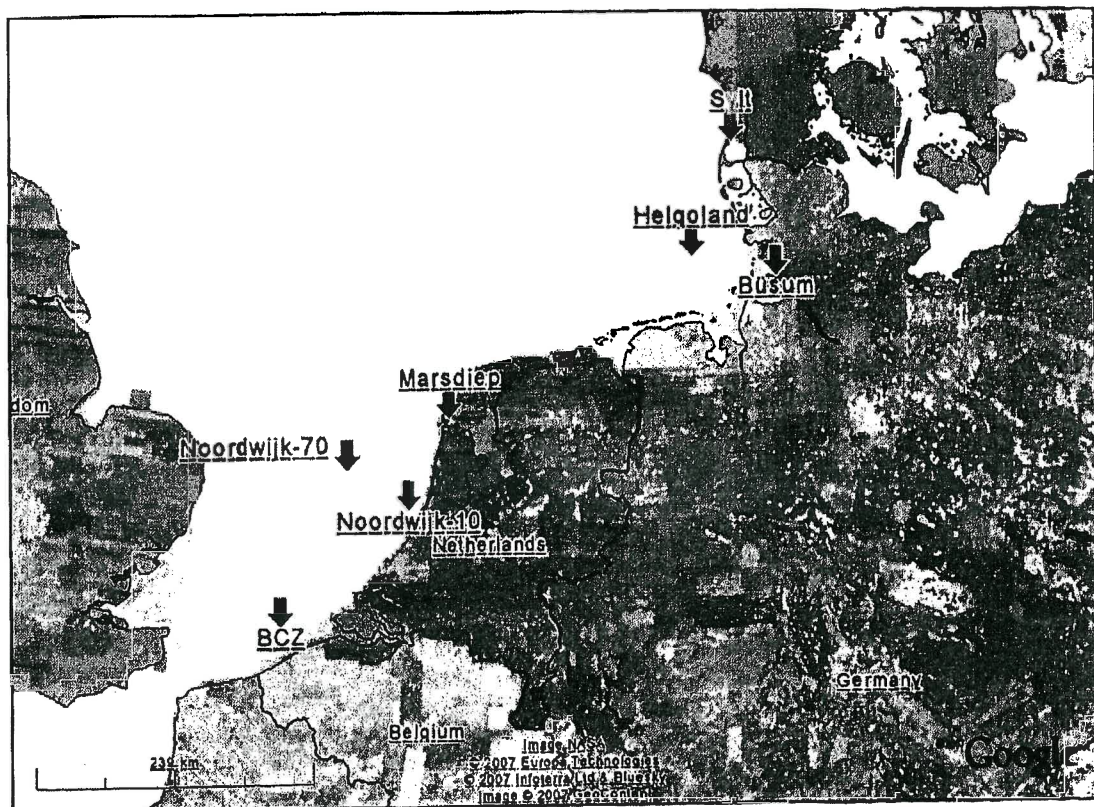


Fig. 1. Map of the European continental coastal zone (North Sea). Investigated sites are indicated by arrows.

Table 1
Study areas, their characteristic features and references

	Belgian coastal zone monitoring sta. 330	Noordwijk-10	Noordwijk-70	Marsdiep sta. N, Nioz jetty	Helgoland Reede	Büsum Mole	Sylt monitoring sta.
Country	Belgium	The Netherlands	The Netherlands	The Netherlands	Germany	Germany	Germany
Geographical location	51°26'0" N / 02°48'5" E	52°15'41" N / 04°24'22" E	52°18'08" N / 04°18'09" E	53°00'18" N / 04°47'42" E	54°11'3" N / 07°54'0" E	54°12' N / 08°84' E	55°02' N / 8.27' E
Mean water depth	20 m	17 m	28 m	3.3 m	7 m	3 m	2.7 m
Salinity	31–34.5	26.5–33	34.5–35.5	28.5–33	28.5–33	26.5–32	26.5–32
Sampling frequency	Spring–fall: weekly winter: twice a week	Weekly	Weekly	Monthly–weekly	Daily (weekdays)	Fortnightly–monthly	Twice a week
Analyzed years	1992–2000	1990–2005	1990–2005	1991–2005	1990–2005	1993–2005	1999–2005
Observed long-term changes in growth limitation	no	yes	yes	no	yes	no	no
References	(Rousseau, 2000; Breton et al., 2006)			(Philippart et al., 2000, 2007)	(Franke et al., 2004; Willshire and Dürselien, 2004)	(Colijn and Cadée, 2003; Tillmann et al., 2000)	(Van Beusekom et al., 2005; Loebel et al., 2007, 2008)

either taken from measurements around the middle of each month, or interpolated from measurements nearest to the 15th. Experimental values of half-saturation constants were not available for all sites. Cloern showed that domains of strong light or nutrient limitation were robust criteria for defining the most potential limiting resource for phytoplankton growth over a wide range of algal physiological variability. We assumed an almost similar species composition in this geographical area and took the half-saturation constants $K_N = 1.5 \mu\text{mol L}^{-1}$ (for DIN uptake), and $K_I = 2.4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (for mean water column irradiance at which growth rate is half the maximum) from Cloern (1999) and furthermore, half-saturation constants $K_P = 0.5 \mu\text{mol L}^{-1}$ (for PO_4 uptake) and $K_{Si} = 5.0 \mu\text{mol L}^{-1}$ (for Si uptake) from White and Dugdale (1997).

Global irradiance data were multiplied by 0.5 to obtain PAR and converted to $\text{mol quanta/m}^2/24 \text{ h}$ based on a conversion factor of $2.77 \cdot 10^{18}$ to obtain the number of quanta/joule (according to Morel and Smith, cited in Kirk, 1994). We altered the procedure of Cloern and took the monthly mean irradiance, instead of the average value from the 3 days around the middle of each month to reduce short-term variability. Secchi depths (S_d) or, if available, suspended matter concentrations (SPM) were either taken from measurements at the middle of each month, or interpolated from measurements nearest to the 15th. Secchi depths (S_d) and SPM were converted into vertical attenuation coefficients (k) using Tillmann et al. (2000): $k = 0.191 + 1.242/S_d$, and a conversion of Loebel et al. (2007) for SPM of the Sylt area, $k = 0.6 + 0.04 \text{ SPM (mg L}^{-1})$. For SPM data of the BCZ we used two conversions of Rousseau (2000 & unpubl.), $k = 0.188 + 0.024 \text{ SPM}$, and $k = 0.08 + 0.05 \text{ SPM}$, respectively, depending on which filter (GF/F or polycarbonate) was used for SPM determination. Then, the mean water column irradiance (E) for each month was calculated by following the formula $E = (E_0/kd)(1 - \exp(-kd))$ (Riley, 1957). Results are presented as contour maps. Interpolations between data points were made by kriging (Surfer 8.0, Golden Software), using a linear variogram without nugget effect.

2.4. Long-term changes in resource limitation

To determine long-term changes in resource limitation, linear regressions were calculated between time and the number of months/year with co-limitation or nutrient limitation. Before, the data were tested for normality using a Kolmogorov–Smirnov test (Statistica 6.0, Stat Soft).

3. Results

Average conditions at the seven stations are shown in Fig. 2 and summarized in Table 2. All mean phosphate concentrations were below $1 \mu\text{mol L}^{-1}$, except for the location Büsum, which showed a value of $2.2 \mu\text{mol L}^{-1}$. Si concentrations ranged from a low of $2 \mu\text{mol L}^{-1}$ to a high of $35 \mu\text{mol L}^{-1}$ at Büsum; offshore stations (Belgian Coastal Zone [BCZ], Noordwijk 70 [NW70] and Helgoland) ranged from 2 to $7 \mu\text{mol L}^{-1}$ and near shore stations ranged around $11 \mu\text{mol L}^{-1}$. High mean DIN was observed everywhere except at station NW70 with a low mean value of $4 \mu\text{mol L}^{-1}$. In the Wadden Sea (Sylt, Marsdiep and Büsum), the range of attenuation coefficients was from 0.7 m^{-1} to about a 2–3 fold higher values. Chlorophyll values ranged from $2.5 \mu\text{g L}^{-1}$ to about 6 to $7 \mu\text{g L}^{-1}$ at both Wadden Sea locations, Sylt and Büsum (Fig. 3), and the near shore station NW10. Published mean chlorophyll levels in the Marsdiep area were also about $7 \mu\text{g L}^{-1}$ (Philippart et al., 2007).

3.1. Sensitivity of phytoplankton growth to light and nutrients

Fig. 4 shows the seasonal dynamics of potential resource limitation during 1990–2005 for seven sites along the European continental coast. Light limitation is compared with limitation by DIN, PO_4 , or Si respectively. From November to February, underwater irradiance limited phytoplankton growth in all areas. Between March and

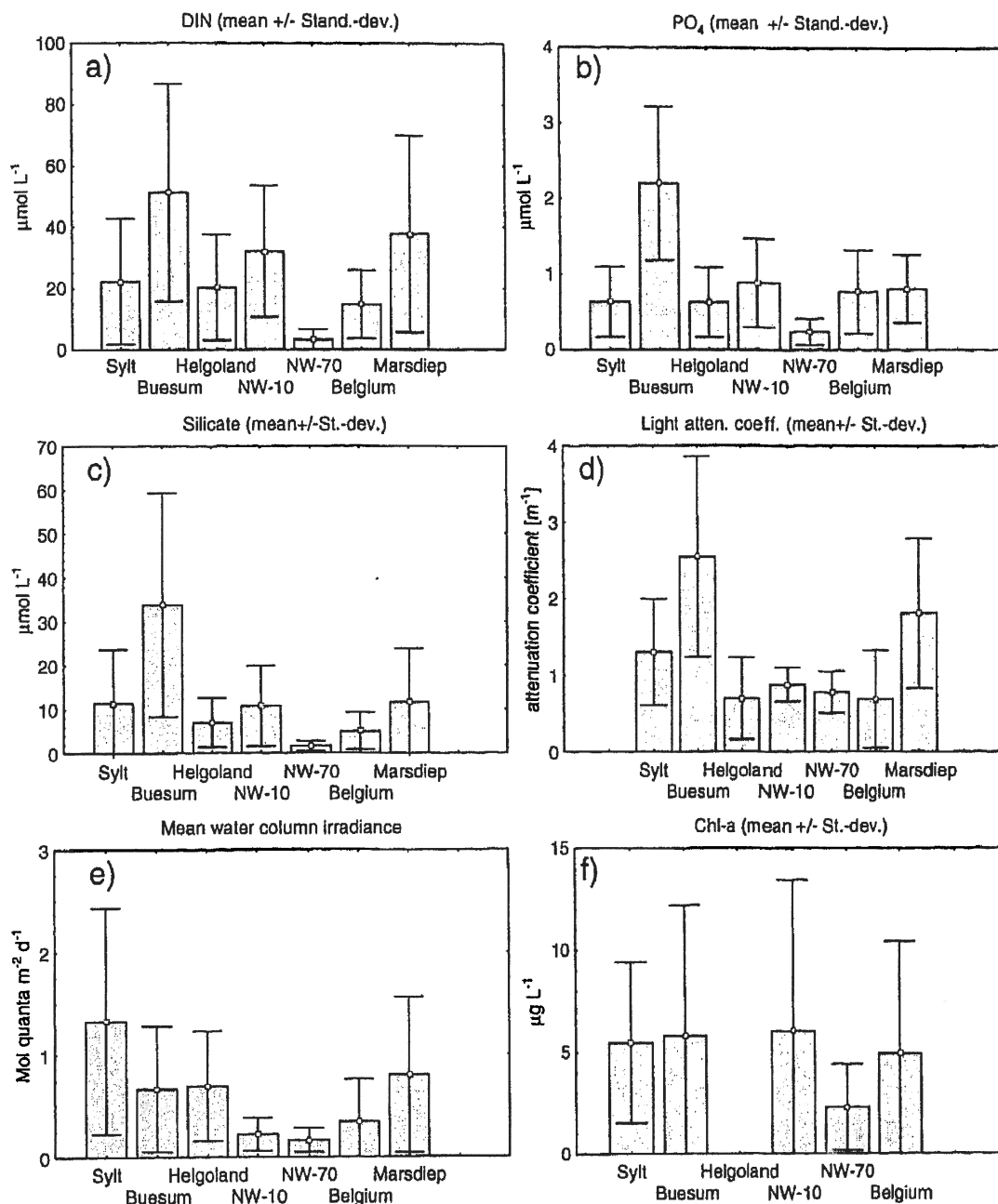


Fig. 2. a–f: Graphs show a) DIN concentration, b) PO_4 concentration, c) Si concentration, d) attenuation coefficient, e) mean water column irradiance, f) Chlorophyll-a concentration. Values are given as means \pm standard-deviation (measurements around the middle of each month, or interpolated from measurements nearest to the 15th. Sites include variable numbers of years as given in Table 1.

October, sites showed different limitation patterns, from 6 months of potential phosphorus limitation at Helgoland in 2004 to almost no nutrient limitation at Büsum. Based on monthly data, nutrient and light limitation periods shorter than 1 month cannot be detected. A clear nitrogen limitation was only observed at Sylt. Here, 2 to 3 months during summer (May–September) showed nitrogen limitation (~17% of all observed months between 1999 and 2005). In the Marsdiep area and at Helgoland, single months of nitrogen limitation occurred (~1–2% of all observed months between 1990 and 2005). At Büsum, NW10, NW70, and the BCZ, only co-limitation by light and nitrogen was observed for single months.

Phosphorus limitation occurred more frequently compared to nitrogen, it was observed between April and August at Sylt (~33% of all observed months between 1999 and 2005) and Helgoland (~31% of all observed months between 1990 and 2005). At NW10, phosphorus limitation was first observed in 1996; from 1998 onward it occurred every year for a period of 1 to 3 months (~17% of all observed month between 1997 and 2005). Phosphorus

limitation occurred in some years at NW70 and in the Marsdiep tidal inlet between April and July (~2% of all observed months at NW70 and ~12% of all observed months in the Marsdiep between 1990 and 2005). At the BCZ and in Büsum, only a single month

Table 2
Mean nutrients, mean water attenuation coefficient K_m , and chlorophyll-a values for the 7 locations studied

Location	DIN	PO_4	Si	K_m	Chl
BCZ	15	0.70	6	0.7	4.5
NW10	32	0.90	11	0.85	6
NW70	4	0.25	2	0.80	2.5
Marsdiep	37	0.80	11	1.80	8
Helgoland	20	0.65	7	0.7	n.d.
Büsum	52	2.2	35	2.5	6
Sylt	22	0.6	12	1.3	5.5

The chlorophyll-a concentration for Marsdiep is based on Philippart et al. (2007). Nutrient concentrations in $\mu\text{mol L}^{-1}$, mean water column attenuation coefficients in m^{-1} , and mean chlorophyll-a in $\mu\text{g L}^{-1}$.

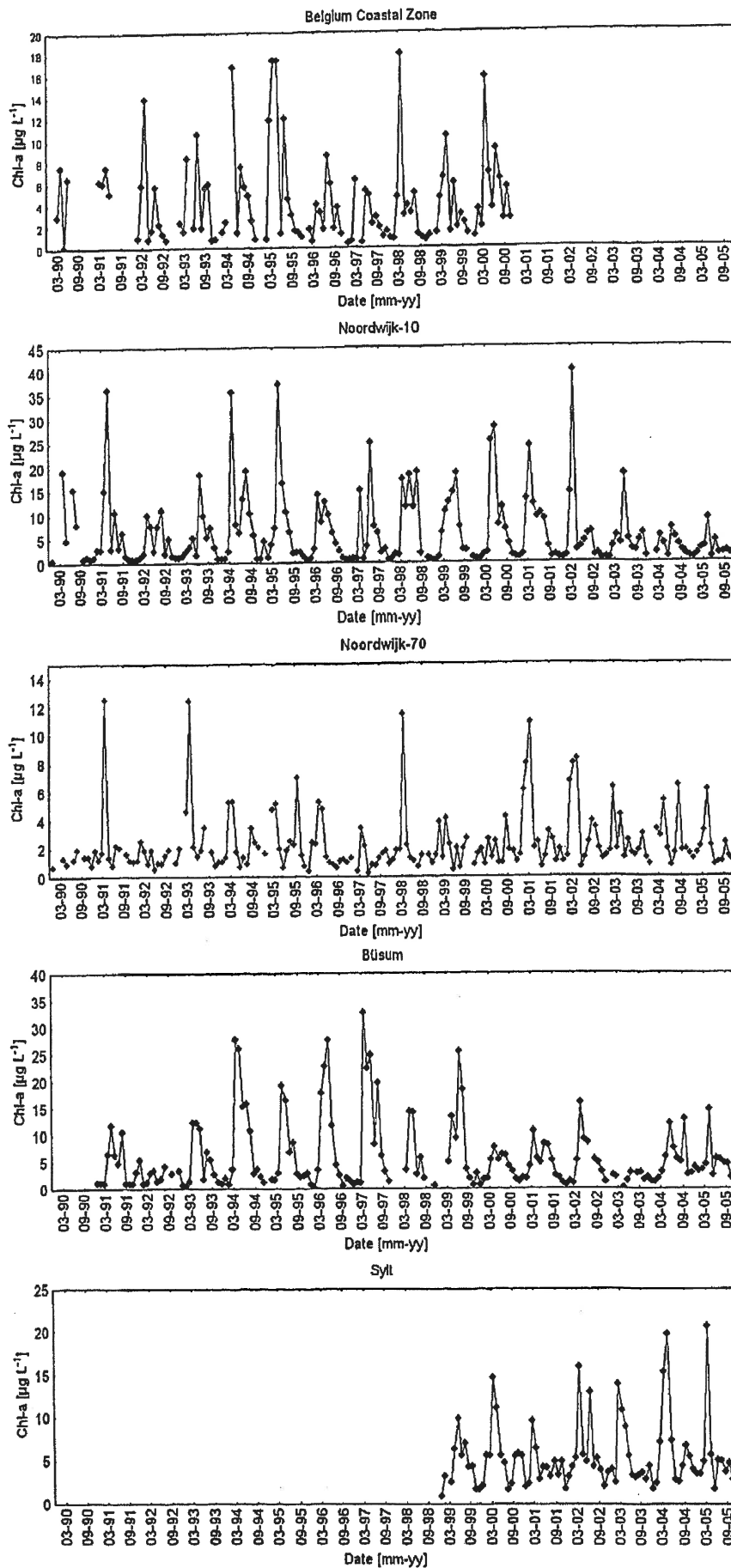
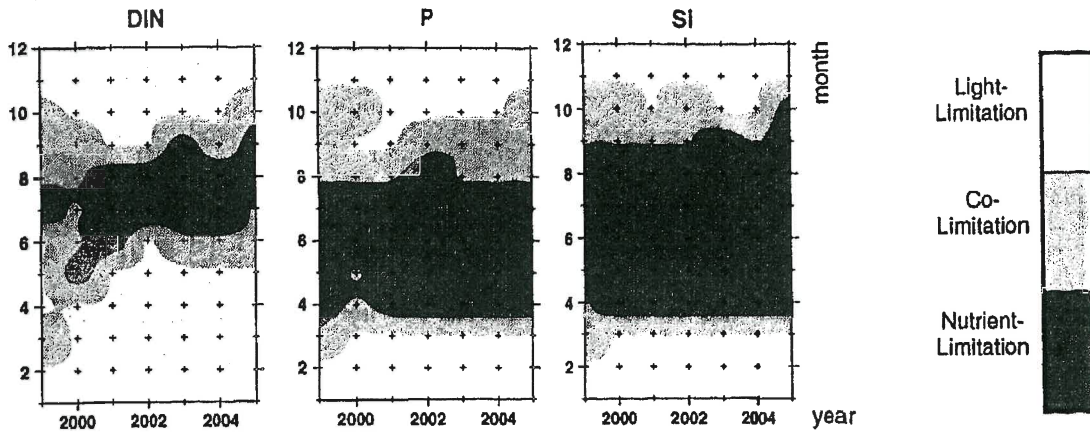
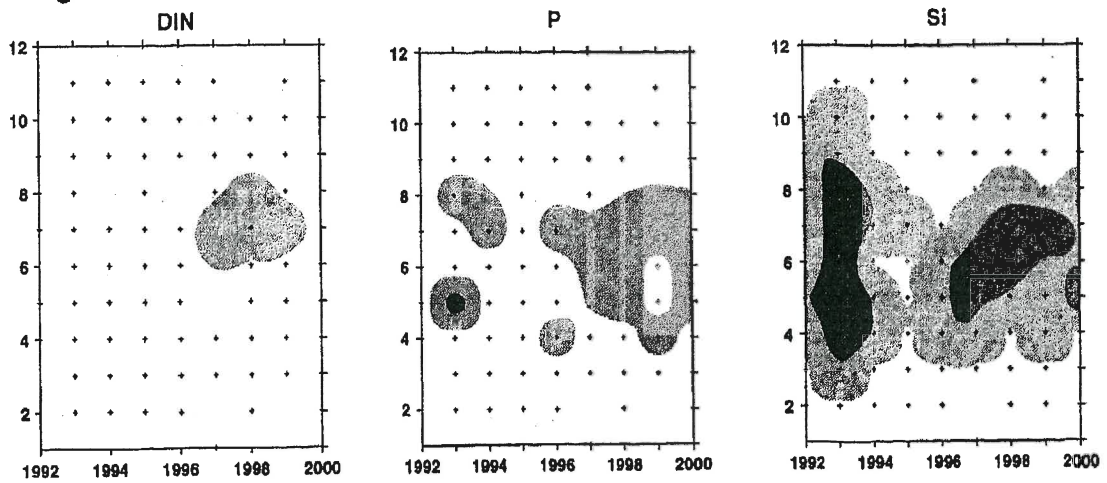


Fig. 3. Chlorophyll-a time series as available, of study sites from 1990–2005. Since measurements were taken in different frequencies, concentrations nearest to the 15th of each month were shown. Note that Y-axes have different ranges.

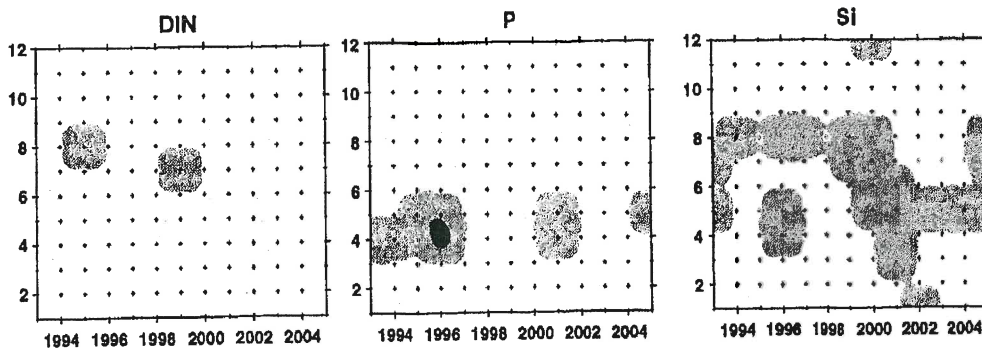
Sylt



Belgium



Büsum



Marsdiep

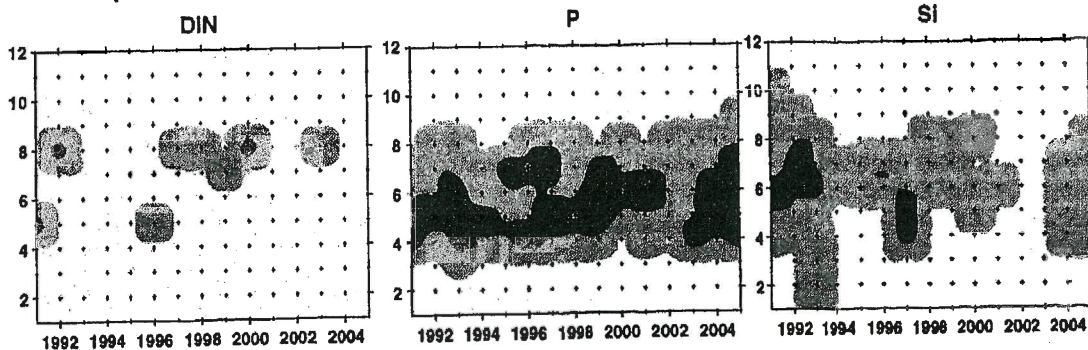


Fig. 4. Potential light and nutrient limitation of phytoplankton growth at seven monitoring stations along the European coastal zone. Contour plots show the seasonal limitation patterns of potential light limitation (white), potential co-limitation of light and nutrients (grey shading) and potential nutrient limitation (dark grey shading) for the investigated years. Data points were indicated by crosses (+).

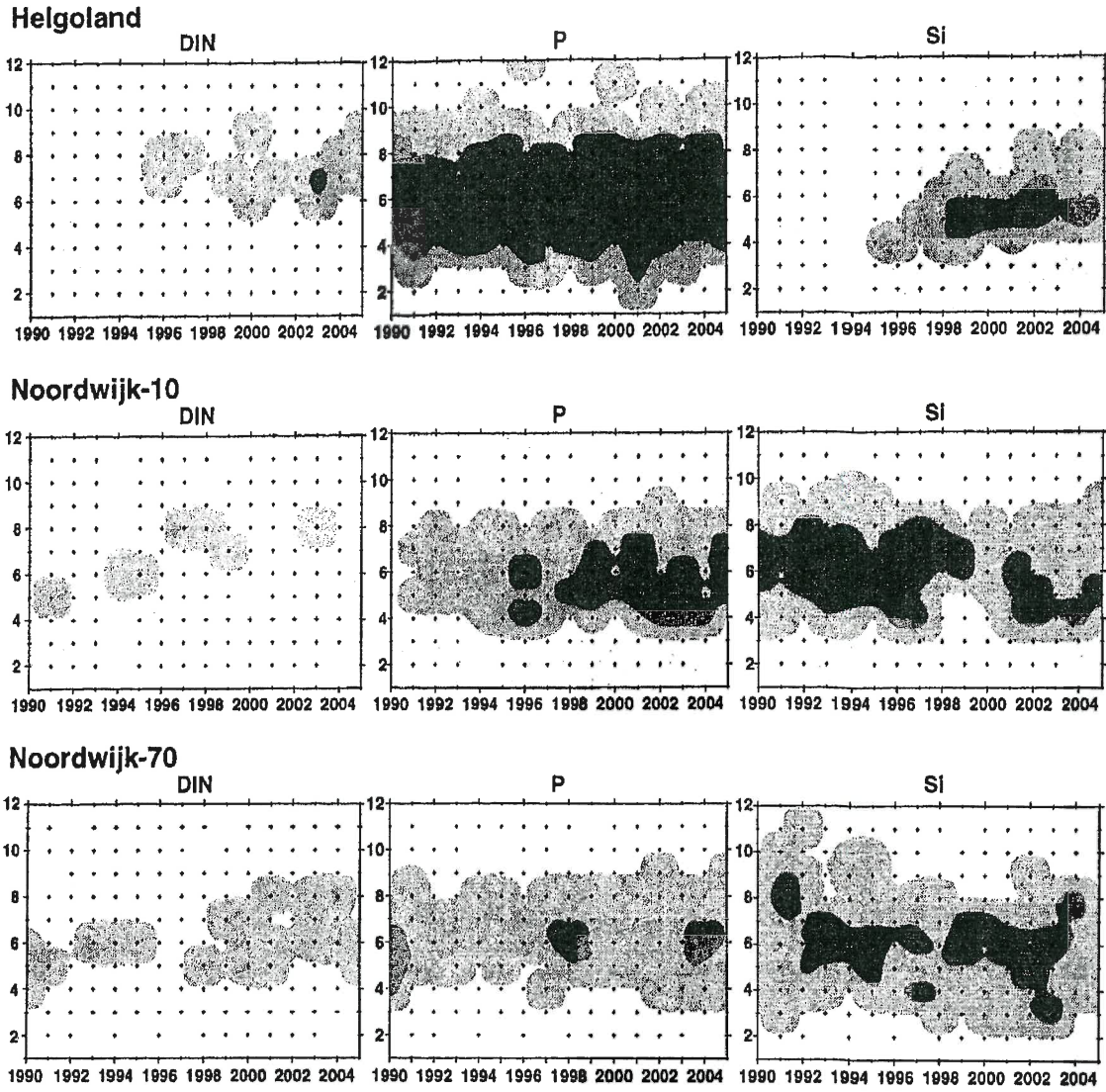


Fig. 4 (continued).

between April and July (Büsum: May) were co-limited by light and phosphorus or limited by phosphorus.

Si limitation occurred at Sylt every year from April to August (~43% of all observed months of 1999–2005). At NW70 and the BCZ, Si limitation occurred in ~15% of all observed months. At Helgoland, in the Marsdiep and at NW10, Si limitation occurred for 1 to 3 months between April and August (up to 9% of all observed months). In Büsum, no Si limitation was observed, however co-limitation of light and Si occurred in ~15% of all observed months between 1993 and 2005.

3.2. Spatial and temporal potential limitation patterns

Fig. 5 summarizes the main potential limitation patterns for the sites analyzed. Except for Sylt, no potential DIN limitation was observed during the periods analyzed (up to 15 years). The present analysis suggests that Si and P are the main potential limiting nutrients along the northwest European continental coast. Si limitation occurred mainly in the period from April to August on all stations except for the turbid station Büsum. P-limitation generally covered a shorter time span with the exception again Sylt and predominantly occurred from May until July, DIN limitation if occurring was limited to a short period, and always occurred after a previous P-limitation, but concomitantly to Si-limitation. The main period was in July and August.

Long-term changes in potential resource limitation (Fig. 6) were observed at Noordwijk-10, Noordwijk-70 and Helgoland. At NW70 a significant increase in numbers of months were observed, where either DIN was limiting or co-limiting ($r^2=0.36, p<0.05$), (Fig. 6a), or PO_4 was limiting or co-limiting ($r^2=0.61, p<0.05$), (Fig. 6b). At NW10, numbers of months where phosphorus was limiting or co-limiting ($r^2=0.59, p<0.05$) significantly increased (Fig. 6c). At Helgoland, a

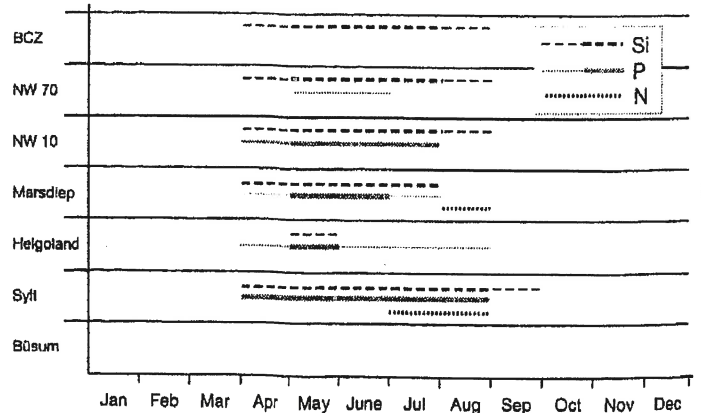


Fig. 5. Annual periods of potential nutrient limitation at the different study sites. Fine lines show overall periods of potential light/nutrient co-limitation. Bold lines show the main periods of potential nutrient limitation.

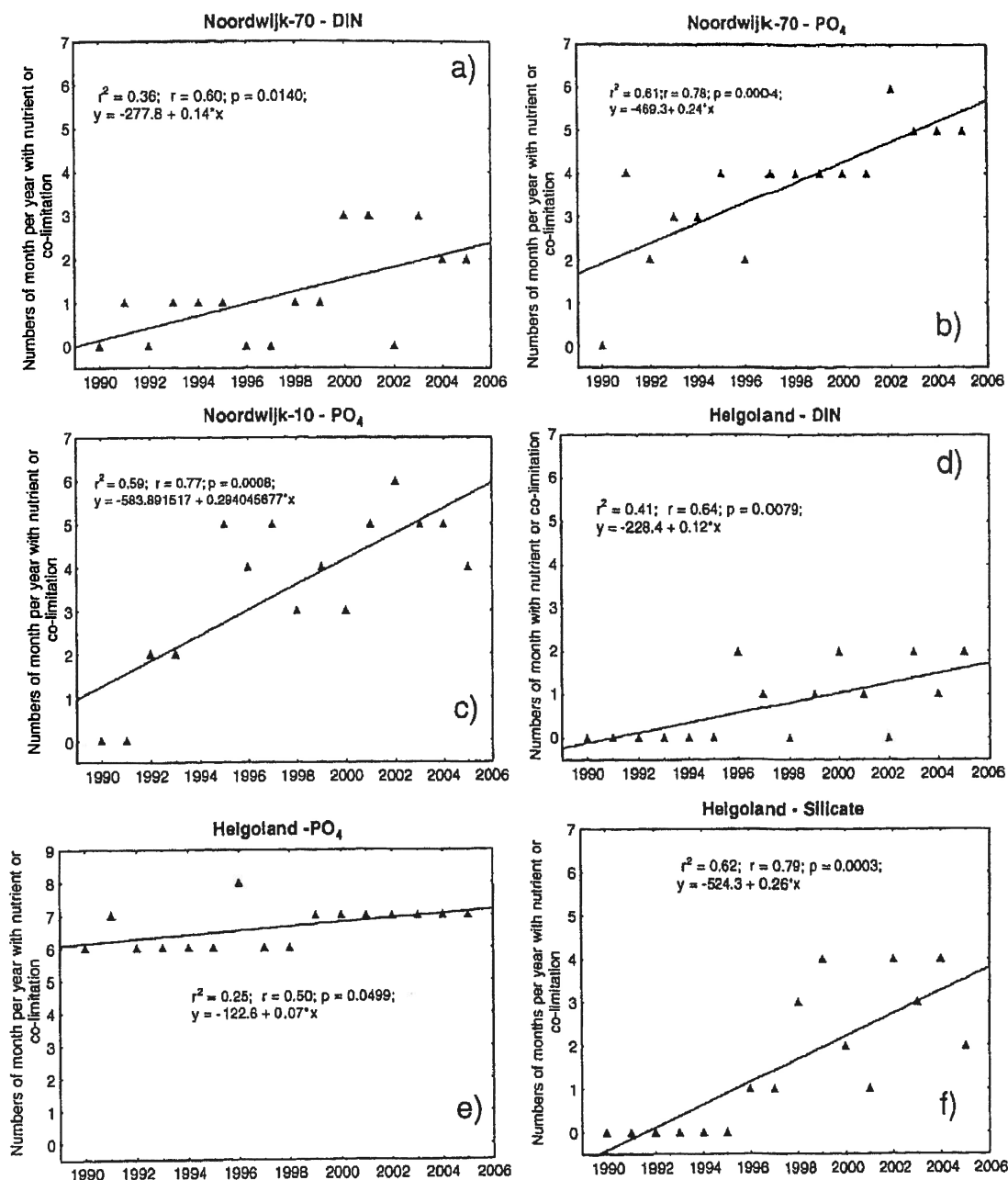


Fig. 6. Significant relationships between numbers of months/year including potential co-limitation or nutrient limitation and time.

significant increase in numbers of months was observed, where DIN was limiting or co-limiting ($r^2 = 0.41$, $p < 0.05$), (Fig. 6d), phosphorus was limiting or co-limiting ($r^2 = 0.25$, $p < 0.05$) (Fig. 6e), and Si was limiting or co-limiting ($r^2 = 0.62$, $p < 0.05$) (Fig. 6f).

4. Discussion

This study compares and addresses potential limitation patterns along the European northwest coast. We used the model developed by Cloern (1999), which is meant to distinguish between potential limiting resources for phytoplankton growth by a set of two parameters: a specific nutrient and the underwater irradiance. This method contains several limitations, including uncertainty to whether or not fixed parameters such as half-saturation constants for nutrients and light can be used over an annual period where species composition and abiotic conditions show large changes. Therefore, one should not use the method in terms of absolute statements on *in situ* limitation, which is already very difficult to measure directly (e.g. Riegman et al., 1990). We suggest to use the resulting patterns of potential limitation only in a comparative manner. Another drawback of the method is that a direct comparison between two specific nutrients is not yet possible.

Given the limited geographical effects on phytoplankton species composition, differences at these locations are small. The seasonal cycle of phytoplankton at the northern and most southern location is rather similar (qualitative phytoplankton composition at Sylt and at BCZ), a diatom dominated spring bloom is followed by both a *Phaeocystis* bloom and mixed blooms of dinoflagellates and diatoms in summer. Given these limitations we argue that general patterns in nutrient and irradiance limitations can be detected and interpreted.

4.1. Potential resource limitation patterns

Whereas no consistent temporal patterns were observed, the spatial potential nutrient limitation patterns seemed to be rather consistent over the years. A direct relationship between DIN concentrations and the total biomass, as shown by the chlorophyll concentrations (Fig. 7) is not obvious. This means that the co-limitation with underwater irradiance plays an important role in the final production of biomass. Retention times of phytoplankton in the whole area are not very different based on residual tidal currents.

Thus, the observed patterns result from different interactions between available nutrients (DIN, PO_4 or Si), water transparency and

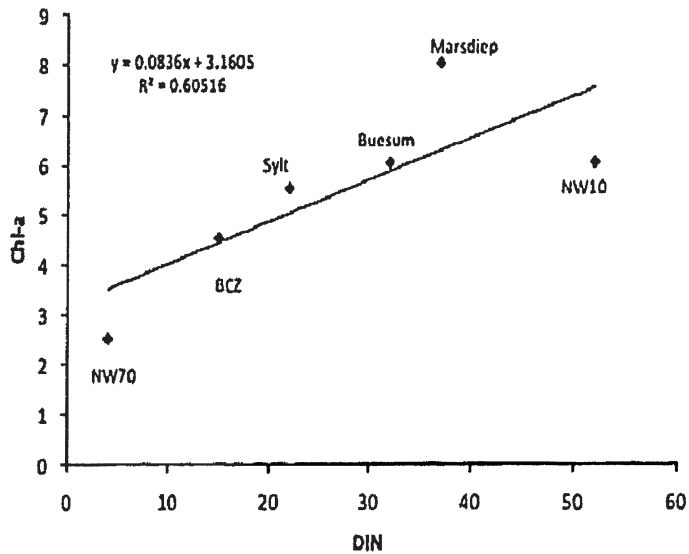


Fig. 7. Mean annual chlorophyll-a concentration ($\mu\text{g L}^{-1}$) of the study sites related to their respective mean annual DIN concentrations ($\mu\text{mol L}^{-1}$).

the mean water depth, which strongly influence the mean water column irradiance. Sylt (highest mean water column irradiance), NW70 (lowest nutrient concentrations), and BÜsum (highest nutrient concentrations) are well suited to exemplify this interaction; high water transparency in the shallow tidal basin at Sylt resulted in high mean water column irradiances, so that nutrients became rapidly depleted during spring and remained limiting until autumn. At NW70, the lowest nutrient concentrations were measured, but light was still the dominant limiting factor, since the mean water depth of ~28 m leads to low mean water column irradiance. Lowest chlorophyll-a concentrations were observed at NW70 (Figs. 2f and 3). At BÜsum, where nutrients from the Elbe river were flushed in more often than other areas of the Wadden Sea (Callies et al., in prep.), the highest nutrient concentrations were measured. However, a turbid water column lead to a distinct light limitation even in summer, so that chlorophyll-a concentrations remained in a mid range compared to the other sites (cf. Tillmann et al., 2000). NW10 showed stronger nutrient limitation during summer than NW70, despite the fact that nutrient concentrations were higher at NW10 (Fig. 2a–c). Mean water column irradiances during summer were higher at NW10 ($0.4 \pm 0.07 \mu\text{mol photons m}^{-2} \text{d}^{-1}$) than at NW70 ($0.28 \pm 0.06 \mu\text{mol photons m}^{-2} \text{d}^{-1}$), (Fig. 2e) leading to less light limitation and therefore to higher nutrient limitation. In winter, mean water column irradiances at NW10 were lower than at NW70, presumably due to sediment resuspension from wind forcing and tidal currents. At the BCZ, light limitation prevailed despite low nutrient concentrations, presumably as a consequence of a turbid and deep water column. Former studies using the approach of Cloern (1999) showed nitrogen limitation during summer in the Oosterschelde in 1991 (Cloern, 1999), and at Norderney in 1990 (Colijn and Cadée, 2003). The Westerschelde in 1991 (Cloern, 1999) and the Ems–Dollard Estuary (inner and outer station) in 1994 (Colijn and Cadée, 2003) clearly had less nitrogen and more light limitation due to a high level of turbidity.

4.2. Comparing potential DIN vs. PO_4 and $\text{Si}(\text{OH})_4$ limitation

Potential P-limitation occurred more frequently than N-limitation (Helgoland, Marsdiep, NW10, NW70, and BCZ). Unfortunately, the analysis proposed by Cloern (1999) does not allow for testing phytoplankton growth limitation between two nutrients (e.g. DIN and PO_4). Thus, if both occur at the same time in one area (mostly at Sylt), we cannot assess whether phosphorus or nitrogen is actually limiting phytoplankton growth. The model of Cloern (1999)

is based on inorganic nutrient concentrations and does not consider organic nutrient forms. It may be possible that faster bacterial turnover rates lower the actual phosphorus limitation; Clark et al. (1998) showed that phosphorus is preferentially regenerated from dissolved organic material than nitrogen is. Also storage of P in sediments (De Jonge and Engelkes, 1993) may partially compensate for P uptake by phytoplankton.

It is commonly suggested whether N or P is limiting phytoplankton growth and production (Howarth and Marino, 2006; De Jong, 2006, pp.197 onward). For the southern North Sea, the BCZ, and for the Western Wadden Sea, phosphorus is frequently discussed as a limiting factor (Skogen et al., 2004; Philippart and Cadée, 2000; Philippart et al., 2007). Our results support the potential limiting role of PO_4 for the BCZ, both stations at Noordwijk (10 and 70), the Marsdiep tidal inlet and Helgoland. At the BCZ, NW10, and NW70, Si limitation was more important than at the Marsdiep tidal inlet or BÜsum. Si input, via Rhine and IJsselmeer to the Marsdiep tidal inlet and by the river Elbe to BÜsum, may play an important role.

4.3. Long-term changes of potential resource limitation

Long-term changes of potential resource limitation were observed in deeper areas: The number of months/year where nutrients were limiting or co-limiting significantly increased at NW70 (28 m, DIN and PO_4) (Fig. 6a,b), at NW10 (PO_4 , 17 m)(Fig. 6c), and at Helgoland (7 m, DIN, PO_4 and Si) (Fig. 6d–f). No changes were observed at the other investigated sites. A significant increase in light limitation was not observed at any site. We restricted this study to the period of 1990 to 2005 in order to compare the data from the different sites. By analyzing longer periods, further trends may be revealed, Loebl et al. (2008) compared nitrogen limitation at Sylt from 1985 to 1992 with the period from 1998 to 2005, and found that the duration of nitrogen limitation during summer was significantly longer in the latter period. The absence of any long-term trends in limitation patterns at the shallow sites suggests that sediments may be involved in masking any trends in nutrient limitation of phytoplankton due to a rapid release of nutrients from the sediment. Recent studies show that a rapid exchange between water and sediment occurs in sandy areas especially (e.g. De Beer et al., 2005).

4.4. Possible impact of nutrient levels and limitation patterns on phytoplankton biomass

The above analysis suggests that especially PO_4 and Si have a high potential to determine the annual phytoplankton biomass. This contrasts with the actual levels of DIN and phytoplankton biomass observed in this study. Lowest phytoplankton levels were found at the low nutrient offshore station NW70; the highest levels found were those at the near shore stations at NW10, and Marsdiep (after Philippart et al., 2007). A tentative relation, shown in Fig. 7, suggests a linear increase of phytoplankton biomass. It also suggests a saturation of mean annual phytoplankton biomass at high DIN levels when chlorophyll-a levels off at mean DIN concentrations of ~30–40 μM . Including the Marsdiep value would suggest a linear increase over the entire range with only BÜsum not reaching potential phytoplankton biomass. The latter is in line with an adverse light climate and a surplus of DIN. PO_4 shows a similar relation with phytoplankton biomass but with more scatter (not shown).

Fig. 7 suggests that, at present, DIN levels may potentially determine the annual phytoplankton biomass levels with the exception of the very turbid stations (attenuation coefficient >2). This is in strong contrast to the potential limitation analysis presented here which showed hardly any DIN limitation (except for Sylt).

As previously mentioned in the introduction, it is currently debated whether N or P is limiting the production levels in the European coastal zone. Unfortunately, the present analysis has not

clarified this debate. On the one hand, a clear dominance in potential P (and Si) limitation was suggested by the model of Cloern. On the other hand, the spatial patterns suggest that DIN is a good predictor of annual phytoplankton biomass, if the water is not too turbid (light extinction <2). Support for the role of nitrogen in determining the annual phytoplankton levels in the Wadden Sea area are given by Van Beusekom et al. (2005). They found a significant correlation between riverine total nitrogen inputs and mean summer chlorophyll levels at three long-term monitoring areas. A recent analysis of the entire Sylt chlorophyll data set (1984–2005) supports the potential role of nitrogen in coastal eutrophication (Van Beusekom et al., 2009–this issue).

5. Conclusion

We applied a method developed by Cloern (1999) to compare potential nutrient and light limitation patterns along the European coastal zone. Our study showed that long-term patterns of potential limitation are consistent and site dependent, and strongly linked to the local hydrography and light conditions of the water column. We found potential limitation patterns repeatedly dominated by potential PO₄ and Si limitation, whereas potential DIN limitation was observed only at Sylt. The latter area was characterized by optimum light conditions, due to a combination of shallow depth and low turbidity, allowing excessive phytoplankton growth and a seasonal development from an early potential PO₄ and Si limitation to a pronounced potential DIN limitation. The spatial pattern of the annual phytoplankton biomass (as chlorophyll) at different sites is best explained by the mean annual DIN levels. We conclude that the model developed by Cloern (1999) is a valuable tool to compare potential limitation patterns, but underestimates the actual role of DIN in limiting the mean annual biomass.

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