

M. Agatz · R. M. Asmus · B. Deventer

## Structural changes in the benthic diatom community along a eutrophication gradient on a tidal flat

Received: 5 October 1998 / Received in revised form: 15 January 1999 / Accepted: 21 February 1999

**Abstract** In the mud- and sandflat region of the outer Königshafen off List on Sylt, the effects of the outflow from a sewage treatment plant on the benthic diatom flora were investigated. The spectrum of shapes, biomass, and diversity was determined in relation to the concentrations of phosphate, silicate, and nitrogen compounds in the overlying and pore water. The biomass increased with the available quantities of nutrients, while the diversity reached a maximum at the intermediate concentrations. Every different set of nutrient concentrations is characterized by a different diatom community. Slight inputs of nutrients led to changes in the relative abundances of forms typical of the habitat. Moderate concentrations permitted the species that are normally present in winter to occur in summer as well. In the strongly eutrophic region, nutrient-loving species that are not locally present under normal conditions formed nearly monospecific populations. A relatively constant input of nutrients almost eliminated the seasonal variations. *Navicula gregaria*, *Nitzschia sigma*, and *Nitzschia tryblionella* proved to be tolerant of pollution, while the genera *Achnanthes* and *Amphora* were typical in the nutrient-poor regions. The nutrient budget, particularly that of the nitrogen compounds, was found to be predominant among the physical and chemical factors.

**Key words** Benthic diatom community · Structural changes · Nutrient concentration · Eutrophication gradient

### Introduction

In the past, the benthic diatom flora was investigated mainly in relation to physical factors, such as characteristics of the sediment, light, and temperature, and more

recently in relation to hydrodynamics (Round 1971; Amspoker and McIntire 1978; van den Hoek et al. 1979; Colijn and Dijkema 1981; de Jonge 1992). The dependence of benthic diatoms upon nutrients has been widely neglected because it was assumed that they were sufficiently supplied from an inexhaustible nutrient pool in the pore water (van den Hoek et al. 1979). Only when the eutrophication problem became acute did the influence of the increased nutrient concentration on the benthic diatoms become the subject of scientific investigations (Van Raalte et al. 1976; Admiraal 1984; Granéli and Sundbäck 1985; de Jonge and Essink 1991; Nilsson et al. 1991; Sundbäck and Snoeijis 1991; Underwood et al. 1998). It became evident that benthic microalgae exerted a strong influence on the nutrient flux between sediment and overlying water (Asmus 1986; Rizzo 1990).

In the freshwater zone, the dependence of benthic diatoms on nutrients has been so unequivocally clarified that the microalgae have been classified according to trophic and saprobity classes and are thus used as sensitive indicators of water quality (Lange-Bertalot 1979; Sládeček 1986). For marine regions, the available knowledge is still far from this level. While benthic marine diatoms as a group show much tolerance to fluctuations in environmental conditions, there is still little knowledge about the physiology and ecology of the individual species (Admiraal 1984). This work is meant to make a small contribution to the knowledge by investigating the effects of the outflow from a sewage treatment plant on the diatom flora. Difficulties in the precise identification of the diatom species due to the considerable methodological difficulties and the need for extensive taxonomic knowledge are certainly an impediment to an extensive investigation of the eutrophication phenomena. Therefore, this work is meant to show from a methodological aspect whether general identifications of the genus, shape, and size spectra combined with simultaneous recording of the morphologically and ecologically outstanding species are sufficient to demonstrate possible variations in the community structure related to the nutrients. Is there a characteristic diatom association for certain degrees of eutrophication?

M. Agatz · R.M. Asmus (✉)  
Wadden Sea Station Sylt, Alfred Wegener Institute for Polar and Marine Research, Hafenstrasse 43, D-25992 List, Germany  
e-mail: rasmus@awi-bremerhaven.de

M. Agatz · B. Deventer  
Fachhochschule Bingen, Department of Environmental Protection,  
Berlinstrasse 109, D-55411 Bingen, Germany

## Materials and methods

### Area of investigation

On the intertidal flats of the "Oddewatt" of Königshafen off the northern part of the island of Sylt, the outflow of a community sewage treatment plant produces a distinct nutrient gradient, which was investigated at sampling sites designated by letters A to D (Fig. 1). Site A is located in the immediate vicinity of the outflow point and is continually washed with the outflowing water, even during low tide. The continual flow there produces sandy sediment. The sites B to D are located at intervals of 150 m. Site D serves as an only slightly influenced reference point on an *Arenicola* sandflat, typical of Königshafen. Along the line formed by sites, the sediment changes from silt at B to mixed sand and silt at C, and to sand at D. Benthic macrofauna (*Hydrobia ulvae*) was present, but it has been shown that the biomass of benthic microalgae was not strongly influenced by grazing on the study sites. All sites were flooded within 30 min and the maximum difference between them in the depth of the flooding was 25 cm.

### Water analyses

The sites were sampled five times at 14-day intervals during the period from 25 June to 22 August 1997. The pore water was sucked through ceramic probes into evacuated glass jars and kept in a deep freezer until analysis. The samples of the overlying water were taken directly above the sediment surface during flood tide in polyethylene jars as well as in Winkler bottles for determination of pH. They were analyzed subsequently in the laboratory. Determinations of phosphate, silicate, nitrite, nitrate, and ammonium were conducted according to the methods of Grasshoff et al. (1983), which required that the pore water samples be diluted up to 20 times their volume with doubly distilled water. The salinity

was determined using a gamma analysis technique salinometer. A WTW pH 191 electrode was used to record the pH.

### Studies of the diatoms

The day after each of the water samples was taken for analysis, twelve random sediment samples were taken at low tide to a depth of 1 cm using a syringe with an open end 1 cm in diameter from within an area of 25 m<sup>2</sup> at each site. Six of these samples served for identification, counting, and measuring cells under a light microscope at a maximum magnification of 100 $\times$ . For this purpose, 4 ml of filtered seawater was added to the samples, and they were shaken. Epipsammic diatoms were loosened from the sediment particles by exposure to ultrasonic vibrations for 2 min, which proved to be sufficient to remove the cells from the sand grains and to suspend the cells in the water as well.

On the days they were taken, two subsamples of each of the three parallel samples were examined under a dark field fluorescent microscope to determine the proportions of living diatoms belonging to each of the shape classes. The other three parallel samples were fixed in formalin. The small diatoms and those appearing in massive numbers were counted in a Thoma chamber. The large and rarer diatoms were counted under an inverted microscope. The specimens were identified using the following literature: van der Werff and Huls (1976), Hendey (1964), Lange-Bertalot and Krammer (1986), Cleve-Euler (1953), and Bertrand (1995).

The diatoms that were counted were measured, and their content of organic carbon was calculated using the factors determined by Asmus (1984) with the formulae of Edler (1979). The second set of six sediment samples was used for photometrical determination of chlorophyll a and pheopigment content after extraction overnight with 10 ml of acetone at 7°C, employing the formulae of Jeffrey and Humphrey (1975) and Lorenzen (1967).

### Statistical evaluation

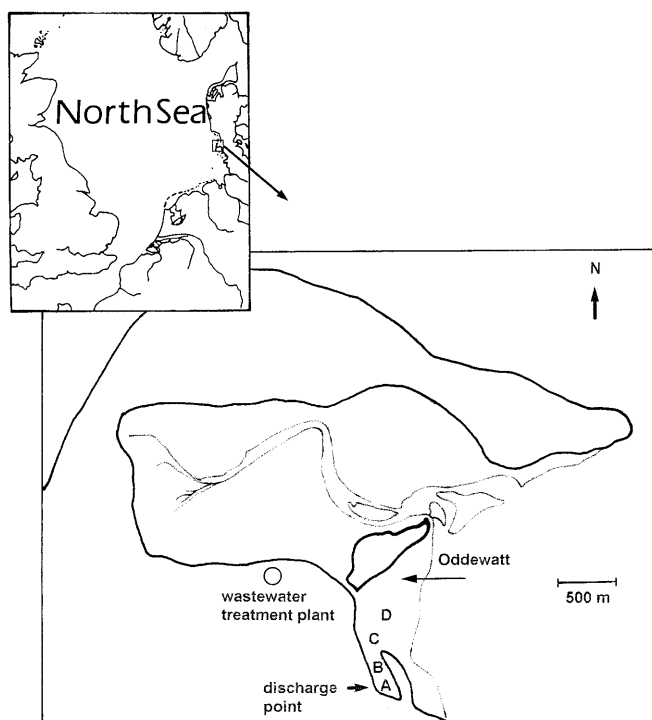
Because the diatom flora requires a certain period of time to react to changes in the nutrient supplies, the dataset for the diatoms was compared with that of the abiotic factors determined 14 days earlier to evaluate their relationship. This time period corresponds approximately to the displacement of the nutrient and biomass curves. Furthermore, Sundbäck and Snoeijs (1991) detected significant changes in the diatom flora in nutrient enrichment experiments only after 14 days.

The statistical analyses were conducted using the relative abundances of the diatoms belonging to the various shape classes so that the temporal variations of the absolute number of individuals could not mask the effects. Discriminant analysis was used to quantify the differences between the sampling sites with regard to nutrient concentrations and diatom flora. Canonical analysis was employed in an attempt to elucidate the relationship between the nutrient supply and the diatom association. In addition, individual correlations were made between all of the diatom shapes and each of the nutrients. Cluster analysis was used to group the diatom forms with similar distribution patterns. The calculations were completed using the computer program Statistica.

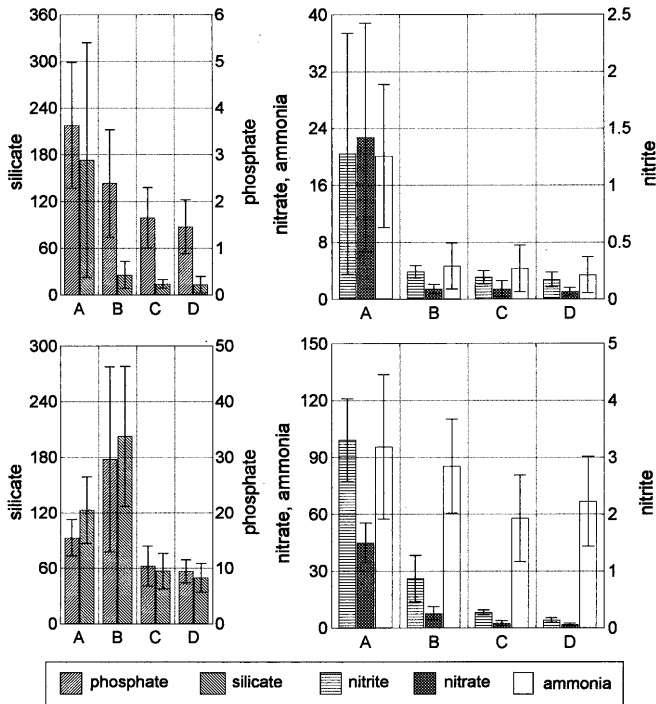
## Results

### Nutrient conditions

Average concentrations over the whole study period showed nearly exponential gradients from the sewage outflow at station A to the sandflat at station D (Fig. 2). If the values at site D are considered to be reference values typical of the region, then site A has to be considered the one subjected to the strongest eutrophication,



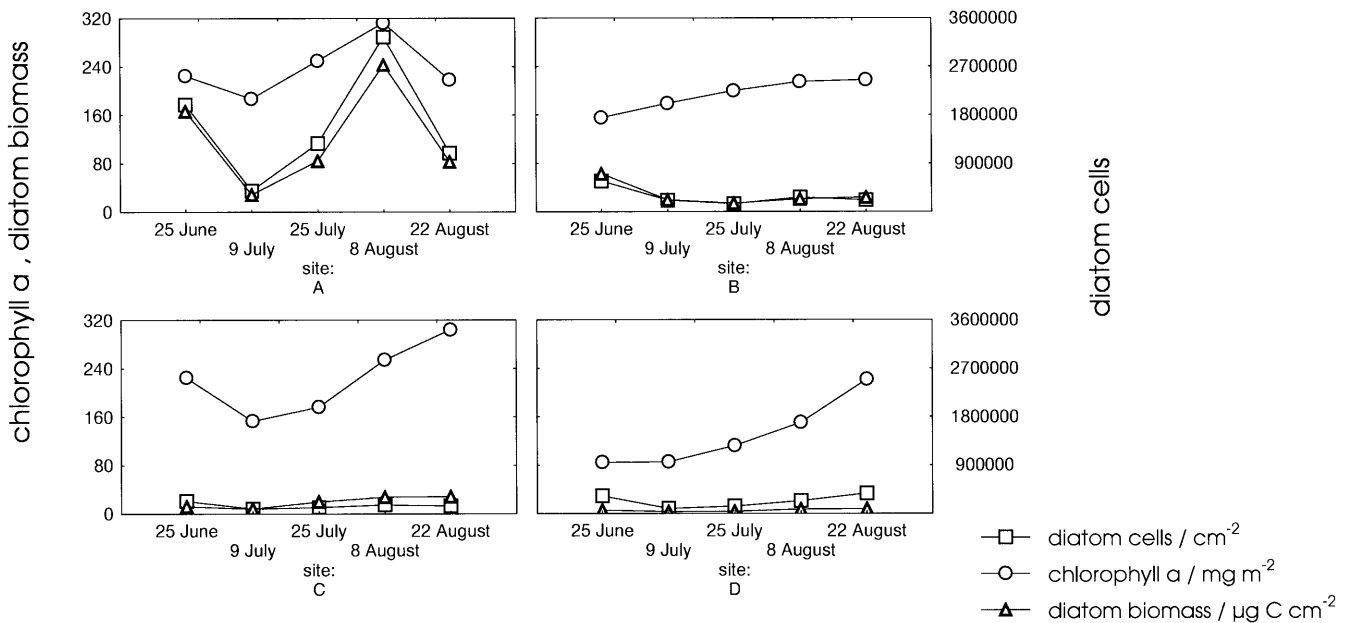
**Fig. 1** Königshafen research area at the northern tip of the island of Sylt. Low water line is indicated (grey line). Sampling sites A to D extend on the tidal flat through the nutrient gradient produced by the outflow from a sewage treatment plant



**Fig. 2** Average nutrient concentrations ( $\mu\text{mol l}^{-1}$  with standard deviations) at sites A to D for the study period June to August 1997. Above Overlying water; below pore water

especially with regard to the nitrogen compounds. The values at site B also tended to be elevated. The large fluctuations in the values result from changes during the study period from June to August in the concentrations in the water flowing out of the sewage treatment plant,

**Fig. 3** Biomass of benthic microalgae at sites A to D during the sampling period



the phase of the tide and the water currents, as well as natural processes. The changes in the mean concentrations of the overlying water along the gradient were different for each of the nutrient substances. While the phosphate value at site A was only 2.5 times the value at site D, the nitrate concentration increased by a factor of 21 over the distance from site D to A. The mean salinity and pH values of 20 PSU and 7.9, respectively, were clearly reduced relative to the other stations (30.5 PSU, pH 8.3) only in the immediate vicinity of the outflow point at site A.

The high mean pore water concentrations at sites A and B were indicative of eutrophication. The mudflat (site B) showed a special affinity for the accumulation of nutrient substances, as shown by observation that the phosphate and silicate concentrations in the pore water were greater at site B than at site A. There was a gradient for nitrogen compounds in the pore water from sites A to D.

In the discriminant analysis, the differences in the nutrient concentrations in the pore water at all sites were significant at  $P < 0.001$ . Only the distance between C and D was not significant. Because of the great degrees of fluctuation in the surface water concentrations, only the differences between site A and the other sites were significant at  $P < 0.01$ .

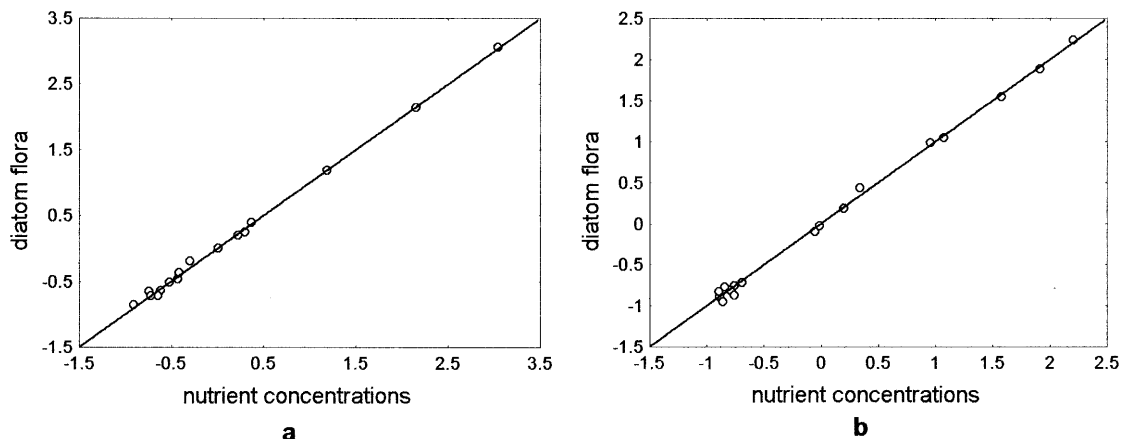
The diatom flora

The composition of the diatom flora was characteristic at each of the sites (Table 1). At site A, *Navicula gregaria* was predominant with an average abundance of 81%, compared to its abundance of 53% at site B. At sites C and D, this species played only a minor role. Species of the genus *Achnanthes* showed the opposite tendencies. Their total abundance rose continually from 4% at site A to 74% at site D. *Nitzschia tryblionella* made a steady contribution to the total number of cells at sites A and B,



**Table 2** Data on diatom flora at sites A to D, arranged at increasing distances from a nutrient-rich outflow.  $H'$  Shannon-Weaver index;  $J$  evenness

Sampling point	Cells ( $10^5 \text{ cm}^{-2}$ )	Biomass ( $\mu\text{g C cm}^{-2}$ )	Chlorophyll a ( $\text{mg m}^{-2}$ )	Pheopigment ( $\text{mg m}^{-2}$ )	Number of diatom forms	$H'$	$J$
A	16.0	120.9	238	94.8	15	0.755	0.279
B	2.8	27.8	193	63.0	14	1.240	0.473
C	1.5	18.4	222	50.4	13	1.390	0.538
D	2.3	5.0	130	5.3	12	0.740	0.292



**Fig. 4** Canonical correlation between composition of diatom flora and nutrient concentrations of overlying water (a) and the pore water (b). Variables of each set (i.e. on one hand the nutrient concentrations and on the other hand abundance of diatom shapes on each sampling date and site) are condensed to an abstract value by weighted sums. These values can then be entered in a normal correlation graph as above. Weights are assigned so that weighted sums will correlate maximally with each other

but the species was difficult to find at C and D. The form group *Navicula* <40  $\mu\text{m}$  reached an abundance maximum (31%) at site C. It amounted to 21% at sites B and D, while it was only 6% at A. The curve of its seasonal occurrence showed a distinct downward dip in the middle of July.

The average proportion of the *Amphora* species remained below 1% and 1% at sites A and B. In contrast, they were important components of the flora at sites C and D, where they also displayed distinct seasonal changes. Before the beginning of sampling in spring, a massive development of these species was observed, but in June and July they were only sparsely represented. In August, they seemed to increase in numbers again.

In general, sites C and D were characterized by more distinct seasonal fluctuations than A and B. At site A, the seasonal changes were largely eliminated by the outflow from the sewage treatment plant. For the species that occurred at low abundances, few tendencies could be detected. *Nitzschia sigma* was found only at sites A and B. *Nitzschia spathula* was generally observed only at site D. Most form classes of diatoms could be observed almost everywhere, at least as isolated individuals. At the nutrient-poor sites C and D, the number of cells of the cyanobacterium *Merismopedia glauca* (Ehr.) Naeg. greatly exceeded that of the diatoms.

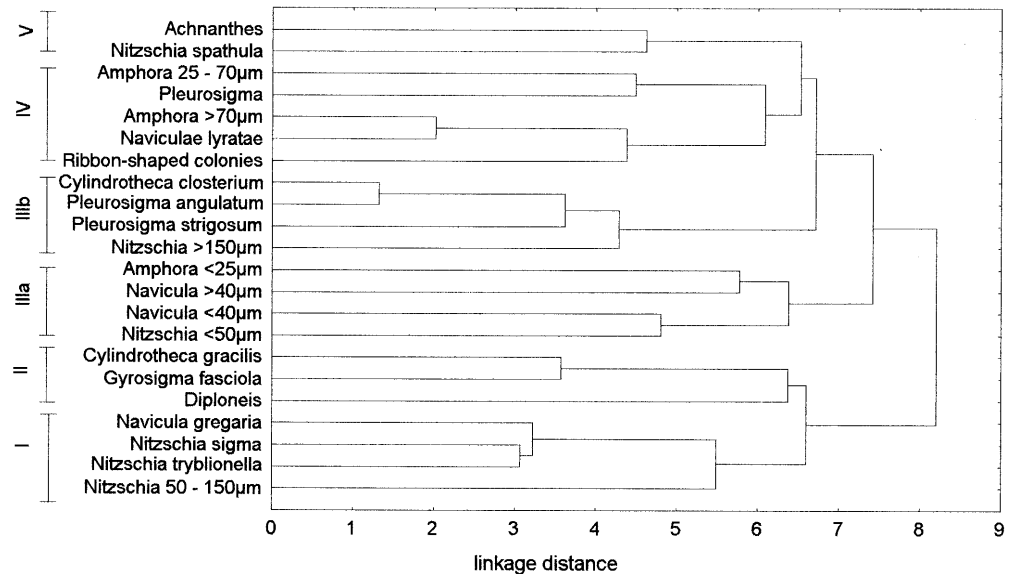
A summary of the parameters and the indices of the diatom flora are provided in Table 2. The chlorophyll a content was at times influenced by the occurrence of *Merismopedia glauca* and is therefore unsuitable for a differential evaluation of the diatom flora. The biomass of the diatoms increased with the increase in nutrient input (Fig. 3), while the diversity was maximal at the intermediate concentration level. The differences in diversity resulted mainly from the relative levels of dominance and not from changes in the number of the forms.

#### Distribution patterns and dependences

The diatom associations at the individual sites were significantly different from one another, as determined at the  $P < 0.001$  level by discriminant analysis. The greatest distance, calculated as the squared Mahalanobis distance, was between B and C, which signifies the transition from the "polluted" region to the "unpolluted" one. The canonical analysis (Fig. 4) encompassed 73% of the variance of the diatom forms, which could be explained by the nutrient conditions in the overlying water to a degree of 48%, equivalent to the total redundancy (canonical  $R = 0.99$ ,  $P = 0.001$ ). The canonical correlation of diatoms with pore water was similar to that of diatoms and the surface water: canonical  $R = 0.99$ ,  $P < 0.001$ , total redundancy of the diatom set of 46%.

The cluster analysis of the distribution pattern of the diatom forms also reflects the nutrient gradient (Fig. 5). In this case, a main distribution can also be recognized, which corresponds to the categories "unpolluted" and "polluted". Classes I and II are clearly distinct, and their species have their centers of abundance at the more eutrophic sites A and B. In addition, the forms of class I

**Fig. 5** Cluster analysis dendrogram of the diatom flora according to their spatial and temporal distribution patterns



are correlated positively with the nutrients and their abundances increase gradually as the nutrient concentrations increase. They can therefore be characterized as nutrient-loving. Class III includes the species that reach their abundance maxima at site C. Its subgroup (a) shows a seasonal minimum at the end of July and beginning of August. In contrast, the fluctuations of subgroup (b) are of an undetermined nature. If one form in this class appears in one place during a particular time of year, however, there is a high probability that the other forms will also be found. Class IV is characterized as a transition between sites C and D. Finally, class V encompasses the forms typical of the unpolluted site D, the abundances of which increase gradually along the gradient with decreasing concentrations. Their correlation with the nutrients can therefore be classified as strongly negative. *Achnanthes*, *Nitzschia spathula*, and, based on the individual correlations, *Amphora* can therefore be assigned to the nutrient-poor region.

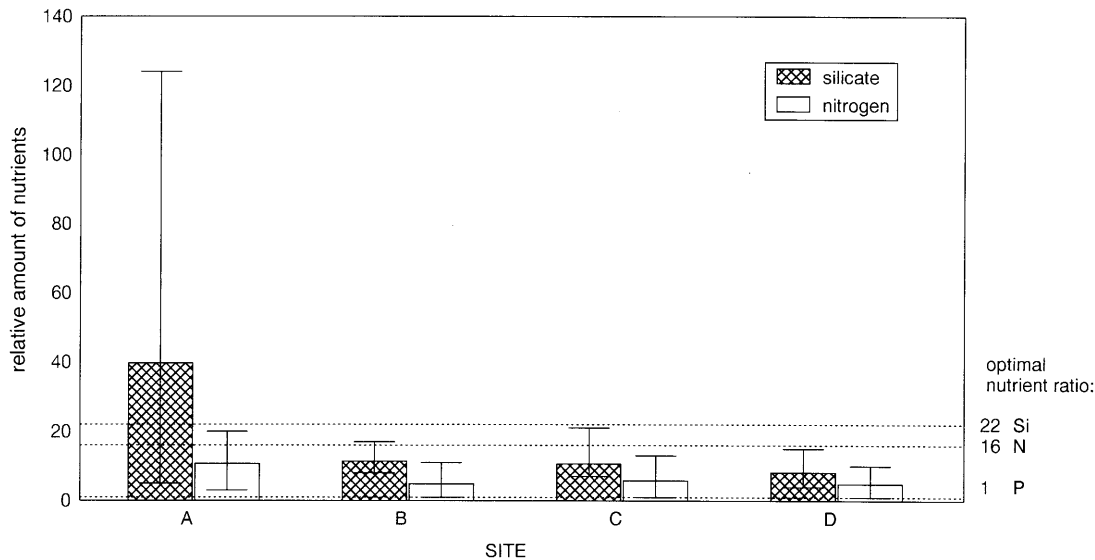
## Discussion

### Sources of nutrients and nutrient limitation

Stefánsson and Richards (1964) reported an optimal Si:N:P ratio of 22:16:1 for diatoms. At site A the corresponding nutrient ratio was almost optimal at 31:20:1 in July (Fig. 6), probably leading to a rapid increase in the diatom biomass. Phosphate seemed to be the limiting factor at site A, as also determined in a region exposed to nitrogen eutrophication by Granéli and Sundbäck (1985). Generally, however, nitrogen is the component lacking in the marine environment (Granéli and Sundbäck 1985), as it was at sites B, C, and D, where the N:P ratio sank to 2:1 in August. Similarly, the relative amount of silicate never reached optimal values. The low Si:P ratio together with the shortage of nitrogen could

have promoted the growth of the cyanobacteria at sites C and D (Patrick 1977). With the increase in the relative amount of silicate in late summer, the diatom biomass increased. This biomass development in spite of a nitrogen shortage suggests that the rich nutrient pool in the pore water was being utilized.

The degree of availability of the pore water and sediment as nutrient sources is still generally unknown (Admiraal 1984). Sundbäck and Granéli (1988) estimated that the microphytobenthos covers between 5 and 30% of its nitrogen requirements by using the pore water. Additionally, the silicate pool of the sediment can be important for benthic diatoms (Nilsson et al. 1991; Sundbäck and Snoeijis 1991). In the present investigation, the mathematical correlations between the diatom forms and the pore water are generally similar to those for the same forms and the overlying water. Species that live mainly at nutrient-poor locations, however, show a stronger dependence upon the pore water. There might be a physiological characteristic that allows certain forms to live at locations poor in nutrients. However, the close relationship may also result from the conditions at the location, which force the diatoms in nutrient-poor environments to rely on the pore water, while those at nutrient-rich sites do not need to do this. Furthermore, from the development of the biomass, it can be inferred that the nitrogen limitation can be reduced by the pore water. However, the utilization of nutrients in the pore water is greatly limited. Simon (1988) made it clear that the nitrate concentrations in the immediate vicinity of the border between the water column and sediment are often lower than those in both the overlying and pore water. Because benthic diatoms inhabit this interface, they are dependent upon nutrient fluxes from both the overlying and pore water into their environment.



**Fig. 6** Nutrient ratios at sites A to D. Silicate and nitrogen are shown in relation to phosphate as reference. Columns represent average values for the study period; Bars indicate minima and maxima

#### Changes in the diatom flora

An increase in the microbenthic biomass with elevations in the amounts of available nutrients has been demonstrated (Cadée 1984; Sundbäck and Snoeijs 1991; Pelletier 1996). However, increases as great as those shown in this study, up to 24 times the reference value, have seldom been found. The significant positive correlation,  $P < 0.01$ , between the biomass and the nutrient quantities further demonstrates the promotional effects.

In this study the association of benthic diatoms changed along the nutrient gradient so that different levels of nutrient loadings could be distinctly separated by statistical analysis. For this purpose it was sufficient to identify the most abundant diatoms. Rare species gave only little further information on the eutrophication level. It is still under discussion on which taxonomic level a system of different diatom associations in relation to the eutrophication level should be based. While Kelly et al. (1995) did not find a significant difference between a system based at either the genus or the species level, Lange-Bertalot (1979) prefers definitely the species level. Within a genus, species may vary in their sensitivity to eutrophication. A study on diatom associations is only possible on the basis of a sound taxonomic knowledge and it is an important target to gain more information on the reactions of specific diatoms on nutrients. However, in this study the identification of the diatoms at the genus level in general and only for very abundant diatoms at the species level seemed to be a feasible compromise in order to gain information on the affect of the eutrophication in a very short time.

Nutrient-poor regions are inhabited mainly by small forms, in this case, species of the genus *Achnanthes*.

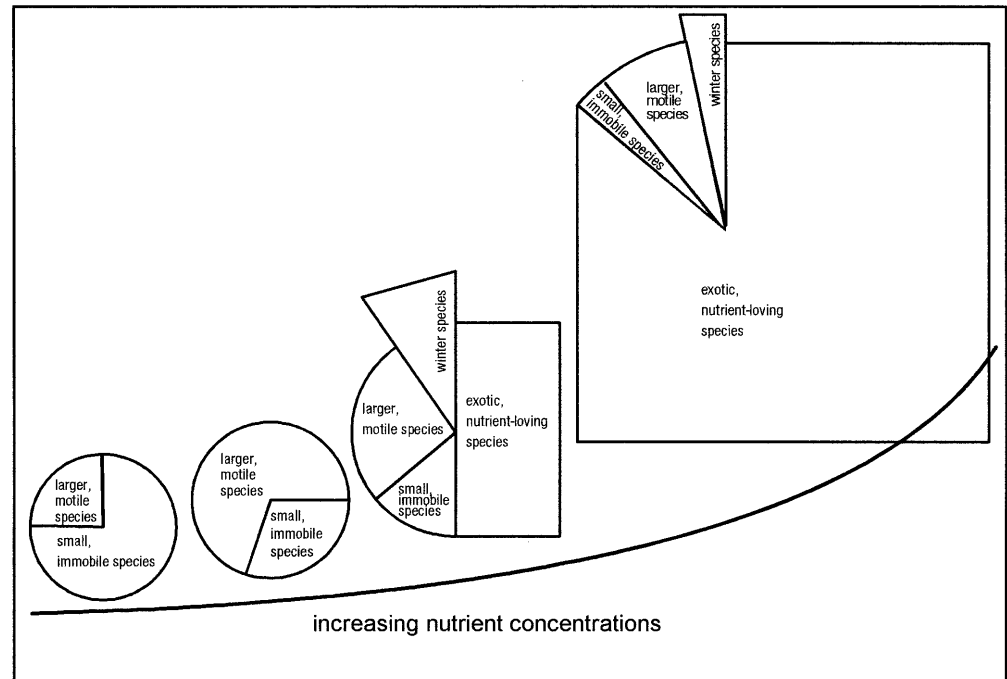
Their great surface to volume ratio permits an intensive nutrient absorption (Baillie 1987), making them especially competitive at nutrient-poor locations (Carrick et al. 1988). In the eutrophic regions, the highly mobile species are predominant: in this case, *Navicula gregaria*. These are able to react to rapid changes in the conditions at their locations, such as a coating of macroalgae, which spread at nutrient-rich locations (Hudon and Legendre 1987).

The diversity variables observed are greater than the comparable values of Asmus (1984) for Königshafen; the actual low  $H'$  and  $J$  values, however, indicate associations that are influenced by a predominance of few species. Although there is a weak negative correlation between diversity and the concentrations of nitrogen compounds, the species richness does not increase continuously along with the nutrient decrease. The maximal diversity at sites B and C can be explained by the promotional effects of the moderate nutrient enrichment, but the kind of sediment is also an important factor since the diversity of diatom associations is lower on sand than on silt (Round 1971). Therefore, the conclusions of Dam (1982) must be preferred, since he denies that there is a uniform relationship between the diversity indices and water pollution. However, a reduction in diversity (Van Raalte et al. 1976) and number of diatom species has been found in enrichment studies in saltmarsh sediments (Sullivan 1976).

The number of forms scarcely varied along the nutrient gradient because isolated individuals of almost all forms could be discovered at all of the sites. Transport processes and the broad ecological amplitude of the diatoms have already been proposed to explain this phenomenon by Lange-Bertalot (1979). However, from the relative abundances of the diatoms, a clear modification due to the nutrient inputs can be recognized (Fig. 7).

The diatom associations at site D conform to the descriptions of those on the sandflats at Königshafen provided by Asmus and Bauerfeind (1994), where the main genera were *Achnanthes*, *Amphora*, *Navicula*, and *Pleurosigma*, while *Cylindrotheca gracilis*, *Diploneis*, *Gyrosigma*

**Fig. 7** Schematized changes in composition of diatom flora observed in summer along the nutrient gradient in Königshafen off List on Sylt. Groups of different species are symbolized by various forms of illustration elements. Biomass is represented by corresponding surface areas. Exotic species mean in this context species that are normally not occurring at the site



*fasciola*, and *Nitzschia* are largely lacking during the summer. The development of *Merismopedia glauca* completes the comparison. The diatom associations described seem to form a characteristic flora of the relatively nutrient-poor *Arenicola* sandflats. Comparable associations of species have also been found in the Dutch Wadden Sea (Colijn and Dijkema 1981). At site C, mainly the same forms are encountered. However, the relative abundances there begin to change, with *Achnanthes* losing its predominance to the small *Navicula* species. *Amphora* and *Pleurosigma strigosum* also begin to become more numerous. This slight shifting in dominance corresponds to the slight increases in the nutrient concentrations.

A more evident change in the diatom community was first observed at site B. *Cylindrotheca gracilis*, *Diploneis*, *Gyrosigma fasciola*, and *Nitzschia*, which Asmus and Bauerfeind (1994) had found only during the winter period of nutrient richness, could be found at this site in summer as well. The nutrient input first promoted the forms that are typical of the habitat but not those typical of the season. This can be explained by the equalizing effect of the wastewater inflow on the nutrient supplies, which become adequate to provide the winter species with their needs for survival even in summer. The natural seasonal fluctuations in the diatom community were reduced in this way.

The influence of the nutrient input at site B leads to even more drastic changes in the diatom flora. *Navicula gregaria*, *Nitzschia sigma*, and *Nitzschia tryblionella*, which do not rank among the spectrum of species typical for the location, appear in great abundance. At the strongly eutrophic site A, the changes are so great that the original diatom community has almost been displaced by a monoculture of *Navicula gregaria*. Wilkin-

son et al. (1986) determined that the dense diatom mats occurring in eutrophic regions are formed almost exclusively of species that normally occur at insignificant abundances.

The principal changes are also apparent from the dataset for the Ems-Dollard estuary obtained during the years from 1977 to 1993 (Peletier 1996). During this period, the amount of the nutrient-rich outflow greatly decreased. First, the predominant nutrient-loving species that had been present during the summer or throughout the entire year were limited to an occurrence in winter, and then they disappeared completely. Among this group are species of *Nitzschia* and *Navicula*, which are similar in form to *Navicula gregaria*. Simultaneously, other species of *Navicula* increased in importance, and new species appeared. *Gyrosigma fasciola* began to appear again in winter instead of summer. Underwood et al. (1998) found that epipelagic species do have different trophic preferences and ammonium may be a factor in determining estuarine species composition of epipelagic diatoms.

This comparison suggests that the principal processes of change in the various regions show no basic differences.

#### Factors with influence

The relationship between the nutrient supplies and the structure of the diatom flora seems to be so close that other factors are overshadowed. The diatom association at the strongly eutrophic sandy site A has a considerably different structure from that at the unpolluted reference site D on sand. It resembles, however, the diatom flora at moderately polluted site B on silt. In the literature, char-



acteristic diatom associations have been described for the different kinds of sediments and the various mud- and sandflat areas (Brockmann 1950; Sundbäck 1983; Asmus and Bauerfeind 1994). According to the results reported here, the influence of the nutrient supplies is so strong, however, that the typical associations can be completely replaced. The dependence of the diatoms on the grain size of the sediment is therefore less strong than their dependence upon the nutrient concentrations. This conclusion is supported by the fact that *Nitzschia sigma* and *Nitzschia tryblionella* reached their maximal abundance at the eutrophic but sandy location, even though Brockmann (1950) and Hende (1964) reported that they seldom appear on purely sand flats.

In a comparison with the salinity, the nutrient supply was found to be a predominant factor, as well. The forms that occurred in massive numbers at the site at which the water was most eutrophic and diluted by freshwater belong to typical brackish-water species. However, they also characterized the diatom flora of the saltwater region with high concentrations of nutrient substances. *Navicula gregaria* and *Nitzschia sigma* are exemplary of these nutrient-loving species. Their preferred salinity normally lies between 30 and 32 PSU (van den Hoek et al. 1979). In this investigation, however, they were most abundant at the eutrophic site that was influenced by freshwater.

The effect of the individual nutrients cannot be considered alone. Because the N:P ratio at the unpolluted reference site was lower than optimal and because it is mainly the amounts of nitrogen compounds that are greatly elevated by the wastewater, it is suspected that the nitrogen supply is the main cause of the observed changes. The individual correlations between the different compounds of nitrogen and the diatom forms were very often and very highly significant. This conforms to the observations in the Ems-Dollard estuary, where similar changes in the diatom flora were observed when there was a strong eutrophication by nitrogen compounds (Admiraal 1980).

In general, it can be confirmed that while the nutrient supply, salinity, and nature of the sediment exert a complex influence on the diatom flora, it is the influence of the nutrient concentrations that is predominant.

**Acknowledgement** Special thanks are due to Charles Hackman for the translation of the German manuscript. This is publication no. 1556 of the Alfred Wegener Institute for Polar and Marine Research.

## References

- Admiraal W (1980) Experiments on the ecology of benthic diatoms in the Ems-Dollard estuary. PhD Thesis, University of Groningen
- Admiraal W (1984) The ecology of estuarine sediment-inhabiting diatoms. In: Round FE, Chapman G (eds) Progress in phyco- logical research 3. Biopress, Bristol, pp 269–322
- Amspoker MC, McIntire CD (1978) Distribution of intertidal diatoms associated with sediments in Yaquina estuary, Oregon. J Phycol 14:387–395
- Asmus R (1984) Benthische und pelagische Primärproduktion und Nährsalzbilanz. Ber Inst Meereskunde, Univ Kiel 131
- Asmus R (1986) Nutrient flux in short-term enclosures of intertidal sand communities. Ophelia 26:1–18
- Asmus R, Bauerfeind E (1994) The microphytobenthos of Königshafen – spatial and seasonal distribution on a sandy tidal flat. Helgol Meeresunters 48:257–276
- Baillie PW (1987) Diatom size distributions and community stratification in estuarine intertidal sediments. Estuar Coast Shelf Sci 25:193–209
- Bertrand J (1995) Contribution à l'étude taxonomique des diatomées; reconnaissance du vivant. Vie Milieu 45:283–293
- Brockmann C (1950) Die Watt-Diatomeen der schleswig-holsteinischen Westküste. Abh Senckenberg Naturf Ges 478:5–26
- Cadée GC (1984) Has input of organic matter in the western part of the Dutch Wadden Sea increased during the last decades? Neth J Sea Res 10:71–82
- Carrick HJ, Lowe RL, Rotenberry JT (1988) Guilds of benthic algae along nutrient gradients: relationships to algae community. J N Am Benthol Soc 7:117–128
- Cleve-Euler A (1953) Die Diatomeen von Schweden und Finnland: Teil III. Kongl Svenska Vetenskapsakademiens Handlingar, Stockholm
- Colijn F, Dijkema KS (1981) Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. Mar Ecol Prog Ser 4:9–21
- Dam H van (1982) On the use of measures of structure and diversity in applied diatom ecology. Nova Hedwigia Beih 73: 87–115
- Edler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Baltic Mar Biol Publ 5:25–31
- Granéli E, Sundbäck K (1985) The response of planktonic and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. J Exp Mar Biol Ecol 85: 253–268
- Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of seawater analysis. Verlag Chemie, Basel
- Hende NI (1964) An introductory account of the smaller algae of British coastal waters, part V: Bacillariophyceae. Ministry of Agriculture, Fisheries and Food, Fishery Investigations Series, HMSO, London
- Hoek C van den, Admiraal W, Colijn F, Jonge VN de (1979) The role of algae and seagrasses in the ecosystem of the Wadden Sea: a review. In: Wolff WJ (ed) Flora and vegetation of the Wadden Sea. Stichting Veth tot Steun aan Waddenonderzoek, Leiden
- Hudon C, Legendre P (1987) The ecological implications of growth forms in epibenthic diatoms. J Phycol 23:434–441
- Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanzen 167:191–194
- Jonge VN de (1992) Physical processes and dynamics of microphytobenthos in the Ems estuary (The Netherlands). PhD Thesis, University of Groningen
- Jonge VN de, Essink K (1991) Long-term changes in nutrient loads and primary and secondary producers in the Dutch Wadden Sea. In: Elliott M, Ducrotoy JP (eds) Estuaries and coasts: spatial and temporal intercomparisons. Olsen and Olsen, Fredensberg, pp 307–316
- Kelly MG, Penny CJ, Whitton BA (1995) Comparative performance of benthic diatom used to assess river water quality. Hydrobiologia 302:179–188
- Lange-Bertalot H (1979) Toleranzgrenzen und Populationsdynamik benthischer Diatomeen bei unterschiedlich starker Abwasserbelastung. Arch Hydrobiol Algal Studies 23:184–219
- Lange-Bertalot H, Krammer K (1986) Bacillariophyceae. Teil 1: Naviculaceae. Gustav Fischer, Stuttgart
- Lorenzen C (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol Oceanogr 12: 343–346
- Nilsson P, Jönsson B, Swanberg IL, Sundbäck K (1991) Response of marine shallow-water sediment system to an increased load of inorganic nutrients. Mar Ecol Prog Ser 71:275–290

- Patrick R (1977) Ecology of freshwater diatoms. In: Werner D (ed) *The biology of diatoms*. Blackwell, Oxford, pp 333–371
- Peletier H (1996) Long-term changes in intertidal estuarine diatom assemblages related to reduced input of organic waste. *Mar Ecol Prog Ser* 137:265–271
- Rizzo WM (1990) Nutrient exchanges between the water column and a subtidal benthic microalgal community. *Estuaries* 13: 219–226
- Round FE (1971) Benthic marine diatoms. *Oceanogr Mar Biol Ann Rev* 9:83–139
- Simon NS (1988) Nitrogen cycling between sediment and the shallow-water column in the transition zone of the Potomac River Estuary. I. Nitrate and ammonium fluxes. *Estuar Coast Shelf Sci* 26:483–498
- Sládeček V (1986) Diatoms as indicators of organic pollution. *Acta Hydrochim Hydrobiol* 14:555–566
- Stefánsson U, Richards FA (1964) Distributions of dissolved oxygen, density and nutrients off the Washington and Oregon coasts. In: Parsons TR (ed) (1984) *Biological oceanographic processes*, 3rd edn. Pergamon Press, Oxford
- Sullivan MJ (1976) Long-term effects of manipulating light intensity and nutrient enrichment on the structure of a salt marsh diatom community. *J Phycol* 12:205–210
- Sundbäck K (1983) Microphytobenthos on sand in shallow brackish water, Öresund, Sweden. PhD Thesis, University of Lund
- Sundbäck K, Granéli W (1988) Influence of microphytobenthos on the nutrient flux between sediment and water: a laboratory study. *Mar Ecol Prog Ser* 43:63–69
- Sundbäck K, Snoeijs P (1991) Effects of nutrient enrichment on microalgal community composition in a coastal shallow-water sediment system: an experimental study. *Bot Mar* 34:341–358
- Underwood GJC, Phillips J, Saunders K (1998) Distribution of estuarine species along salinity and nutrient gradients. *Eur J Phycol* 33:173–183
- Van Raalte CD, Valiela I, Teal JM (1976) The effect of fertilization on the species composition of salt marsh diatoms. *Water Res* 10:1–4
- Werff A van der, Huls H (1976) *Diatomeeënflora van Nederland*. Otto Koeltz Science Publishers, Koenigstein
- Wilkinson M, Fuller I, Rendall D (1986) The attached algae of the Clyde and Garnock estuaries. *Proc R Soc Edinburgh* 90B: 143–150

Communicated by K. Lüning