Spatial patterns of benthic diatoms, carbohydrates and mud on a tidal flat in the Ems-Dollard estuary

Natascha Staats[1,3], Eric M.G.T. de Deckere[2,5], Ben de Winder[1,4] & Lucas J. Stal[2]

[1]*Department of Microbiology/ARISE, University of Amsterdam, Nieuwe Achtergracht 127,*
1018 WS Amsterdam, The Netherlands
[2]*Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, P.O. Box 140, 4400 AC Yerseke,*
The Netherlands
[3]*Present address: Max Planck Institute for Marine Microbiology, Celsiusstrasse 1, D-28359 Bremen, Germany*
[4]*Present address: Ministry of Public Works, RWS-Directie Zeeland, Koestraat 30, 4331 KX Middelburg,*
The Netherlands
[5]*Present address: University of Antwerp, Department of Biology, Universiteitsplein 1, 2610 Wilrijk, Belgium*

Abstract

The chlorophyll *a* content and two operational fractions of carbohydrate (water extractable and EDTA extractable) were measured every three months during one year along transects on a tidal flat in the Ems-Dollard estuary (The Netherlands). Chlorophyll *a* was used as an indicator of microphytobenthos biomass, which was composed predominantly of epipelic diatoms. Both carbohydrate fractions correlated significantly with chlorophyll *a*. EDTA extractable carbohydrates were more resistant towards degradation than the water extractable fraction. During most of the year, concentrations of chlorophyll *a* and carbohydrates were low, but in June, high concentrations of up to 90 μg chlorophyll *a*/g sediment were found in a narrow zone running parallel to the channel. Maximum concentrations of water extractable carbohydrates and EDTA extractable carbohydrates ranged between 800–1200 and 600–800 μg/g sediment, respectively. The mud content was high ($\pm$ 90%) at the margin of the tidal flat. This was not limited to the growth season of the diatoms, but was observed throughout the year. This indicated that the high mud content at the mudflat margin was mainly caused by hydrodynamic factors, and not by biostabilization. In June, exceptionally high diatom densities were found in sediment with a high mud content. There was only minor evidence that biostabilization by epipelic diatoms lead to a further increase in the mud content of the sediment.

Introduction

Transport of cohesive sediments in estuaries is strongly affected by sedimentation and erosion of sediment particles on tidal flats. Erosion of sediment occurs whenever the shear stress exerted on the bed by waves or currents exceeds a threshold value, known as the critical bed shear stress for erosion. The critical bed shear stress depends on physical factors, such as dewatering due to evaporation, rainfall and consolida-

tion (Anderson, 1983). In addition, there is increasing evidence that several biological processes have an impact on the critical bed shear stress (Montague, 1986; Dade et al., 1990; Paterson, 1997).

An important biological process is the secretion of extracellular polymeric substances (EPS) by epipelic diatoms. When the sediment surface is covered by a biofilm of cells and polymers (mainly polysaccharides), sediment particles are trapped in the exopolysaccharide matrix. It has been shown that this process
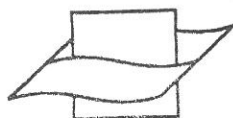
Vlaams Instituut voor de Zee
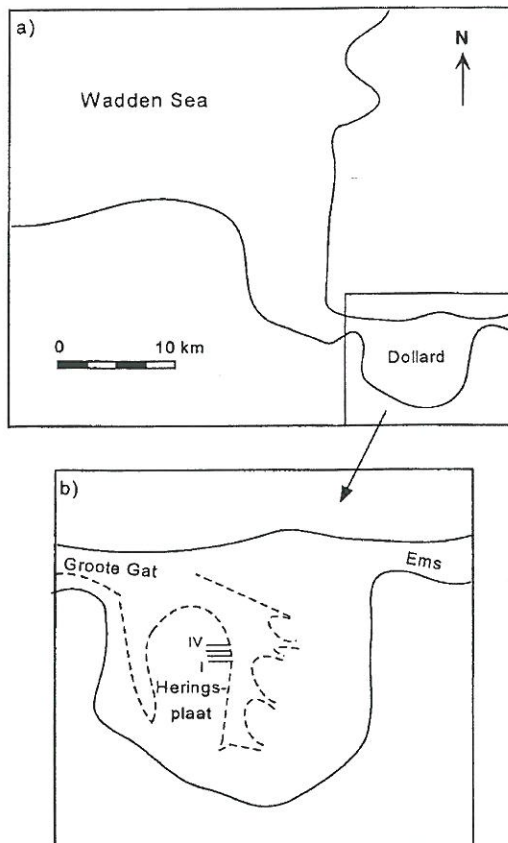*Flanders Marine Institute*

Figure 1. Ems-Dollard estuary (a) and Dollard (b) indicating the approximate location of transects I–IV on the Heringsplaat. Dotted line indicates mean low water mark.

substantially increases the resistance of the sediment bed against erosion (Holland et al., 1974; Grant et al., 1986; Paterson, 1989; Sutherland et al., 1998).

On the Heringsplaat, a tidal flat in the Ems-Dollard estuary (The Netherlands) (Fig. 1), Kornman & De Deckere (1998) observed that the stability of the sediment bed was highest in the April–June period, when the density of benthic diatoms was also highest. In order to assess the impact of benthic diatoms and exopolysaccharide on sediment stability and transport, more information is needed about the spatial distribution of benthic diatoms and associated exopolysaccharides. Several reports deal with spatial distribution of microphytobenthos on tidal flats. For instance, Cadée & Hegeman (1977) and Guarini et al. (1998) assessed the consequences of spatial variability of microphytobenthos biomass for estimates of

primary production. Brotas et al. (1995) and Colijn & Dijkema (1981) studied the relationship between microphytobenthos and sediment characteristics. They showed that diatom concentrations were correlated to the mud content of the sediment. However, no information on carbohydrates was provided in these reports. Therefore, a sampling program was carried out along transects located on the Heringsplaat. In this paper, we report on the distribution of diatoms, carbohydrates and mud along these transects.

Materials and methods

Study area and sampling

Study area

The Ems-Dollard estuary (500 km^2) is situated in the N-E part of the Dutch Wadden Sea. The Dollard (approx. 100 km^2) is the upper reach of the Ems-Dollard estuary (Fig. 1) and consists ±85% of intertidal mudflats. Measurements were performed on the Heringsplaat, located in the central part of the Dollard (Fig. 1b).

Sampling

In 1996, samples were taken at 3-monthly intervals along two to four transects running perpendicular to the channel. The transects were numbered I–IV, from south to north and were 50 m apart and approximately 250 m long (Fig. 1b). Samples for analysis of carbohydrates, chlorophyll *a* and grain size were taken using stainless steel corers of 1.75 or 2.40 cm diameter. The corer was pushed into the sediment, closed airtight with a rubber stopper and lifted. Each transect contained nine sampling points, at 20 m intervals for the five lowest points and 40 m intervals for the other points, with the lowest sampling point at 20 m from mean low water. Sampling was done in triplicate. The cores were subsectioned into three slices (0–5, 5–10 and 10–20 mm). The triplicate core samples of corresponding depths were pooled. Samples were stored at −20 °C immediately after slicing.

For correlations of chlorophyll *a*, carbohydrates and sediment mud content, additional data were used. These were collected monthly in 1995 and 1996 from 3 or 2 plots of 100 m^2, respectively, and from three transects sampled in 1997. The transects were sampled each month from April to October at three points. Cores were taken in triplicate and the top 5 mm was pooled. The 100 m^2 plots were located close to the

transects, and were sampled at monthly intervals. In 1995, sampling was done in triplicate (not pooled) on three plots and only the top cm was used. In 1996, two plots were sampled in triplicate (not pooled) and cores were sectioned into 0–5, 5–10, 10–15 and 15–20 mm slices.

Analyses

Extraction and analysis of carbohydrate
Sediment samples were freeze-dried prior to the determination of carbohydrate. To 100 mg of dry sediment, 1 ml of distilled water was added. Samples were incubated for 1 h at 30 °C, followed by centrifugation for 5 min at 20 000 g. In order to extract more more tightly bound carbohydrates, the pellet was subsequently extracted with 1.5 ml of 100 mm Na_2-EDTA for 12 h at 20 °C, followed by centrifugation for 5 min at 20 000 g (Underwood et al., 1995). The carbohydrate concentration in the water extract and the EDTA extract was determined using the phenol/H_2SO_4 assay with glucose as a reference (Dubois et al., 1956).

Extraction and analysis of chlorophyll a
Chlorophyll a was extracted from freeze-dried sediment by N,N-dimethylformamide (DMF) (Porra et al., 1989). After addition of 0.7 ml DMF to 100 mg of sediment, the samples were incubated for 1 h in the dark. After centrifugation for 5 min at 20 000 g, the absorption of the extract was determined spectrophotometrically at 665 nm. Phaeophytin was determined by acidification by adding 15 μl HCl (5 M) to 0.5 ml DMF extract and measuring absorption at 665 nm. Concentrations of chlorophyll a and phaeophytin were calculated according to the following equations (De Winder et al., 1999):

$$\text{chlorophyll } a \text{ (g l}^{-1}) = k \cdot (E_n - E_a)/A$$

$$\text{phaeophytin (g l}^{-1}) = k \cdot (R \cdot E_a - E_n)/A,$$

where E_n is extinction of neutral extract, E_a is extinction of acidified extract, A is absorption coefficient of chlorophyll a in DMF and K and R are constants. Values for A, K and R in DMF were 72.114, 2.3 and 1.8, respectively, and were experimentally obtained using purified chlorophyll a and phaeophytin (De Winder et al., 1999).

Grain size
Grain size was analyzed with a Malvern particle sizer 3600 EC.

Statistical analysis
Level of significance of correlations between variables was analyzed with the Spearman rank correlation coefficient (r_s) (Sokal & Rohlf, 1981). For significance testing between sampling seasons, Friedman's method for randomized blocks was used (Sokal & Rohlf, 1981). The transect data could not be pooled because not all transects were sampled in all seasons, and because in some instances significant differences were observed between transects (also tested with Friedman's method for randomized blocks, data not shown). Instead, pairwise comparisons between seasons were made for the transects sampled in those seasons (Table 1).

Results

High concentrations of chlorophyll a (up to 90 μg/g sediment) were found in June (transects I and III), whereas in March, October and December concentrations were low: less than 10 μg/g sediment (all transects) (Fig. 2a). Microscopic observations of fixed sediment samples indicated that the phototrophic community consisted primarily of epipelic diatoms. The high chlorophyll a concentrations in June were observed between approximately 50 and 150 m from the channel. Within 50 m from the channel and at distances greater than 150–200 m, concentrations along the transects sampled in June decreased to less than 20 μg/g sediment. The same pattern was observed for the water extractable carbohydrate fraction (Fig. 2b). Concentrations of EDTA extractable carbohydrates were also higher in June (up to 800 μg/g sediment), but compared with chlorophyll a or water extractable carbohydrates, the differences in concentrations between June and other sampling periods were less pronounced (Fig. 2c). In addition, the concentration of EDTA extractable carbohydrates was also relatively high close to the channel and at increasing distance from the channel, compared with the zone between 50 and 150 m. This spatial pattern suggested that EDTA extractable carbohydrates were less closely linked to chlorophyll a than water extractable carbohydrates, however this was not apparent from correlation coefficients between both carbohydrate fractions

Table 1. Level of significance of differences between seasons for all variables in the upper 5 mm, sampled along transects in 1996

		March	June	October
chlorophyll *a*	June	$p<0.05$		
water extr. carbohydrate		$p<0.005$		
EDTA extr. carbohydrate		$p<0.005$		
mud content		ns ($n=16$)		
chlorophyll *a*	October	$p<0.005$ ($n=31$)	$p<0.01$ ($n=17$)	
water extr. carbohydrate		ns ($n=31$)	$p<0.005$ ($n=17$)	
EDTA extr. carbohydrate		$p<0.005$ ($n=31$)	$p<0.005$ ($n=17$)	
mud content		ns ($n=33$)	ns ($n=16$)	
chlorophyll *a*	December	ns ($n=17$)	ns	ns
water extr. carbohydrate		ns ($n=17$)	ns	ns
EDTA extr. carbohydrate		ns ($n=17$)	$p<0.005$	$p<0.005$
mud content		$p<0.01$ ($n=18$)	ns ($n=8$)	ns ($n=17$)

n: number of data.
ns: not significant.
For design of statistical analysis: see 'Materials and methods' section.

and chlorophyll *a* (Fig. 3). Water extractable carbohydrates correlated significantly with chlorophyll *a* ($p<0.01$; $r_s=0.21$; $n=161$), but not when data from the transects sampled in June were omitted ($r_s=0.12$; $n=146$) (Fig. 3a). The correlation of EDTA extractable carbohydrates with chlorophyll *a* was also significant ($p<0.001$; $r_s=0.46$; $n=159$) (Fig. 3b), and remained significant when the data from the June 1996 transects were omitted ($p<0.001$; $r_s=0.45$; $n=143$).

Table 1 lists the results of significance testing between seasons. These confirmed the differences between June and other seasons: significant differences were found for all variables except mud content when June was compared to March or October (the lack of significance for chlorophyll *a* and water extractable carbohydrates when June was compared to December can probably be attributed to the small size of the dataset (Table 1)).

At low concentrations of chlorophyll *a*, no clear depth distribution could be observed, but in the zone of of high chlorophyll *a* concentrations in June, chloro-

phyll *a* was almost completely restricted to the top 5 mm of the sediment (Fig. 4a). The same pattern was observed for water extractable carbohydrates (Fig. 4b). In contrast, EDTA extractable carbohydrates were found in similar concentrations throughout the top 2 cm of the sediment even in the zone of high concentrations found in June (Fig. 4c).

The mud content in the upper sediment layer decreased with increasing distance from the channel (Fig. 5). In most cases, this was a more or less gradual decrease, however transect III sampled in June showed a slightly different pattern, when the landward gradual decrease in mud content was interrupted by a zone of high mud content, coinciding with the zone of high chlorophyll *a* concentrations (50–150 m from the channel, cf. Figs 5 and 2a). However, significance testing yielded no significant differences in mud content between data obtained in June and other sampling periods (Table 1). When chlorophyll *a* was plotted against mud content (Fig. 6), it became clear that high values of chlorophyll *a* were only found only
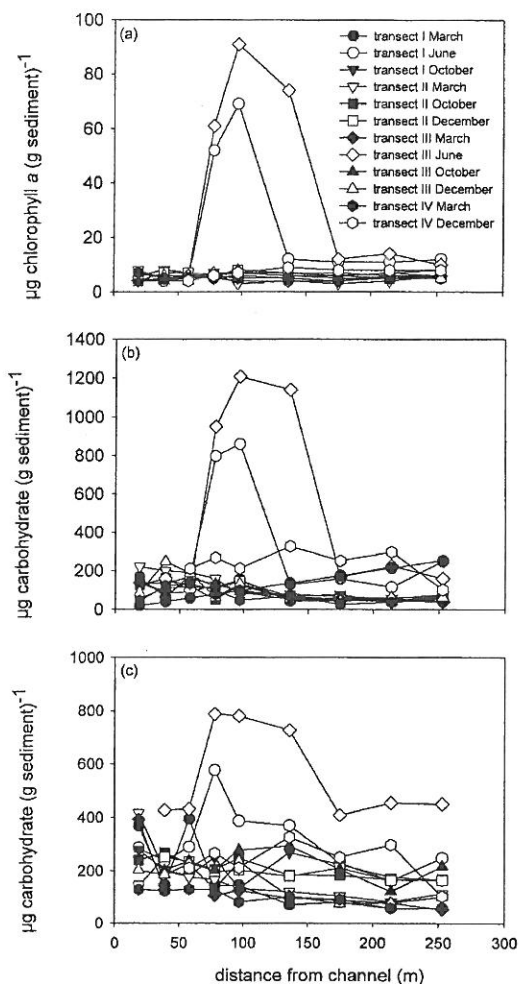
Figure 2. Chlorophyll *a* (a), water extractable carbohydrates (b) and EDTA extractable carbohydrates (c) in the upper 5 mm along transects sampled on 5 March, 26 June, 6 October and 4 December 1996.
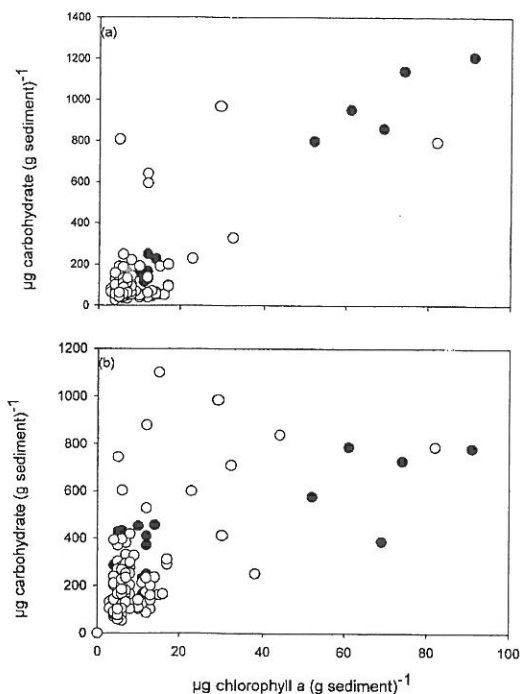

Figure 3. Water extractable carbohydrates (a) and EDTA extractable carbohydrates (b) in the upper 5 mm (data from 1995: upper 10 mm) plotted against chlorophyll *a*. Closed symbols are data from June 1996.

at high mud values. In contrast, a broad range of mud content values was observed at low chlorophyll *a* concentrations. There was no significant correlation between chlorophyll *a* concentration and mud content both when the data from the transects from June 1996 were included (r_s=0.01; n=158) or when these were omitted (r_s=−0.06; n=142).

Discussion

In June 1996, the concentrations of chlorophyll *a* and carbohydrates on the Heringsplaat were much higher than during the rest of the year. Several observations confirmed that this period represented an exceptional situation: water extractable carbohydrates correlated significantly with chlorophyll *a* only when the data from June 1996 transect were included. Also, a clear depth distribution of chlorophyll *a* and water extractable carbohydrates was only observed in this period. Seasonal differences in standing stock and productivity have frequently been observed for microphytobenthos on tidal flats in the Dutch Wadden Sea (Cadée & Hegeman, 1974; Colijn & Dijkema, 1981; Admiraal et al., 1982). However, these are also subject to large interannual variations, since concentrations of chlorophyll *a* and carbohydrates were much higher in 1996 than in 1997 (data not shown).

Since the phototrophic community consisted predominantly of epipelic diatoms (Wiltshire et al., 1998), chlorophyll *a* could be regarded as a good indication of benthic diatom biomass. Furthermore, the close coupling of water extractable carbohydrates with chlorophyll *a* in June 1996 suggested that this fraction consisted of carbohydrates secreted by benthic
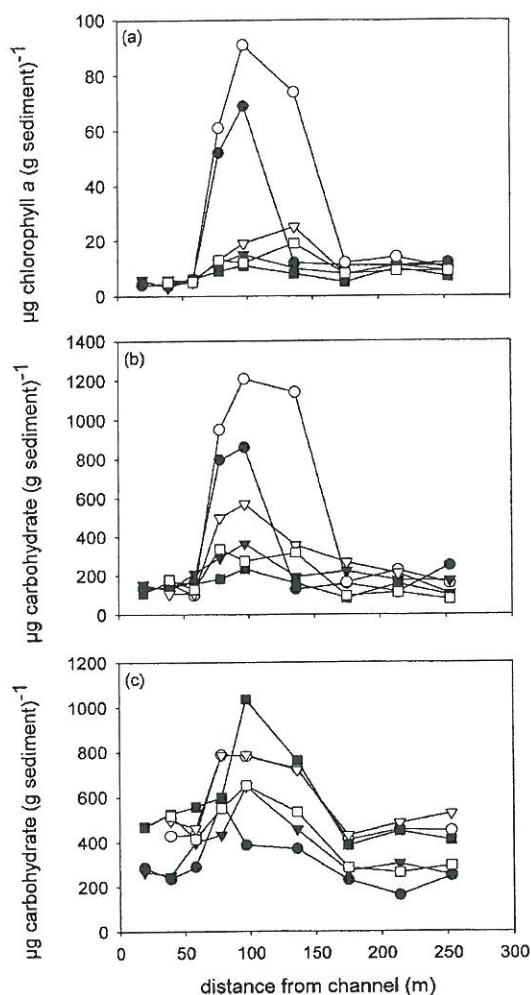
112

Figure 5. Mud content in the upper 5 mm along transects sampled on 5 March, 26 June, 6 October and 4 December 1996. Legend to symbols as in Figure 2.

Figure 6. Chlorophyll *a* in the upper 5 mm (data from 1995: upper 10 mm) plotted against mud content. Closed symbols are data from June 1996.

Figure 4. Chlorophyll *a* (a), water extractable carbohydrates (b) and EDTA extractable carbohydrates (c) along the transects sampled in June 1996 (closed symbols: transect I, open symbols: transect III) at depths of 0–5 mm (circles), 5–10 mm (triangles) and 10–20 mm (squares).

diatoms. A strong coupling of water extractable carbohydrates and chlorophyll *a* in fine-grained sediments was also observed by Underwood & Paterson (1993a) and Underwood & Smith (1998). The EDTA extractable fraction, consisting of carbohydrates more closely bound to the sediment (Underwood et al., 1995), also significantly correlated with chlorophyll *a*, suggesting that these carbohydrates were produced by benthic diatoms as well. The fact that concentrations of EDTA extractable carbohydrate were relatively high when chlorophyll *a* was absent (i.e. at increasing distance
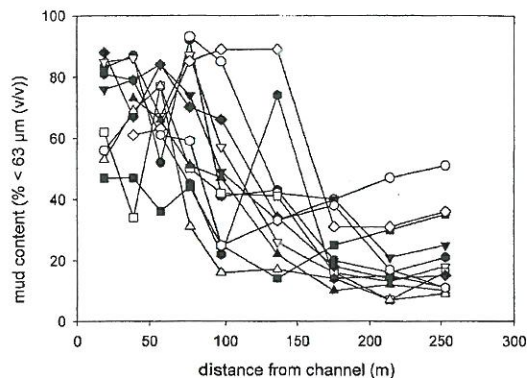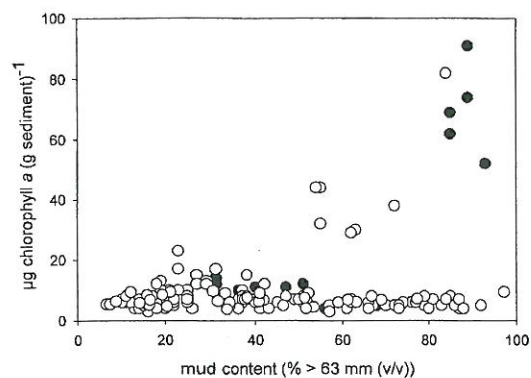
from the channel or at greater depths), indicated that this fraction was more resistant towards degradation than water extractable carbohydrates. This is in agreement with De Winder et al. (1999), who also found that the ratio of EDTA extractable carbohydrates to chlorophyll *a* increased with depth.

Generally, on tidal flats grain size decreases with increasing elevation due to lower current velocities (Postma, 1957; Coles, 1977). This has been observed on several tidal flats in the Ems-Dollard estuary (Colijn & Dijkema, 1981; Delgado et al., 1991) including the Heringsplaat (Schröder & Van Es, 1980), and on the Molenplaat in the Westerschelde (Barranguet et al., 1997). Contrasting with these findings, we observed an area of high mud content on the margin of the Heringsplaat, which has also been reported for some other tidal flats (Postma, 1957; Vos et al.,

1988). High mud concentrations found on the edge of a tidal flat in the Wash (England) were ascribed to accretion of mud by diatoms (Coles, 1977). However, our data showed that mud content on the margin of the Heringsplaat was high throughout the year. This phenomenon could, therefore, not be explained by binding of mud by diatoms. More likely, the high mud content was caused by hydrodynamic factors. Current velocity probably decreased from the channel to the flat, which may have resulted in high sedimentation rates (H. Ridderinkhof, pers. comm.). Also, wave action, which is generally low at the edge of a mudflat (Postma, 1957; Frostick & McCave, 1979; Anderson, 1983; De Jonge & Van Beusekom, 1995) could play a role. Postma (1957) concluded that the margin of a tidal flat in some cases may be considered an area of low hydrodynamic energy because of low wave action.

There was a distinct spatial distribution in chlorophyll *a* and carbohydrate concentrations on the Heringsplaat. In June, the density of benthic diatoms was high in the area characterized by a high mud content. Vos et al. (1988) observed the same phenomenon on tidal flats in the Eastern Scheldt: in spring a dense population of epipelic diatoms developed at the margin of the flat. Epipelic diatoms only seem to reach high densities in muddy sediment (Colijn & Dijkema, 1981; Sundbäck, 1984; De Jonge, 1985; Brotas et al., 1995; De Jong & De Jonge, 1995; Guarini et al., 1998). Also, they are generally encountered in more elevated areas of low hydrodynamic energy (Sundbäck, 1984; Vos et al., 1988; Underwood & Paterson, 1993b; Brotas et al., 1995; De Jong & De Jonge, 1995). Possibly, diatom densities and mud content correlate as a result of low hydrodynamic energy (Sundbäck, 1984; De Jong & De Jonge, 1995) since epipelic diatoms are easily resupended when exposed to conditions of high hydrodynamic energy (Delgado et al., 1991; De Jonge & Van Beusekom, 1995). On the other hand, epipelic diatoms may select for sediment of low grain size. On sediments of different grain size, typical assemblages of microphytobenthos are often found (McIntyre & Moore, 1977; Amspoker & McIntyre, 1978). Moreover, Watermann et al. (1999) observed that, in monocultures, the benthic diatoms *Nitzschia* sp. and *Phaeodactylum tricornutum* achieved higher densities on mud than on sand. The reason for a preference for muddy sediment may be found in the higher concentrations of inorganic nutrients in muddy sediment than in sandy sediment. It has also been suggested that photoperiod length may be an important factor, since at elevated areas photoperiods are longer than in lower areas (Pinckney & Zingmark, 1991). However, the high densities observed at the margin of the Heringsplaat indicated that the length of the photoperiod was not a major factor controlling the presence of epipelic diatoms. It is likely, therefore, that diatom growth was controlled by low resuspension rates and/or high mud content.

Kornman & De Deckere (1998) showed that sediment stability at the margin of the Heringsplaat was higher during the period of high diatom biomass and high concentrations of carbohydrate (April–June) than during the rest of the year. Some of our data confirm these observations, since in June there appeared to be a broadening of the zone of high mud content, coinciding with the zone of high diatom biomass and high carbohydrate concentrations. Apparently, in the area where during the rest of the year mud was removed, erosion was prevented in June by the presence of the diatoms. This observation indicated that there may be an interaction between mud content and diatom growth. Van De Koppel (pers. comm.) observed a positive feedback between mud content and diatom growth based on both mathematical modelling and experimental evidence. However, this effect was observed only along one of the two transects sampled in June, and did not lead to a significant enhancement of mud content compared to other sampling periods. Moreover, biostabilization by epipelic diatoms seemed to be restricted to areas of relatively low hydrodynamic energy, which appears to be contradictory to the widely accepted hypothesis that biostabilization by diatom films greatly affect estuarine sediment fluxes (Coles, 1977; Underwood & Paterson, 1993a; Underwood, 1997). In order to establish the impact of biostabilization by benthic diatoms on sediment fluxes compared to hydrodynamic factors, the large body of field data available should be used in modelling experiments.

Concluding, an area of very high mud content was observed on the margin of the Heringsplaat throughout the year, also when diatom densities were low. Therefore, the mud content in this area was determined by hydrodynamic factors. Diatoms and exopolysaccharide exhibited a clear seasonal and spatial distribution, with high concentrations only in early summer (June) and in the area of high mud content, indicating that the presence of diatoms is dependent on sediment mud content. We observed no strong effect of biostabilization on mud content of the sediment.

References

Admiraal, W., H. Peletier & H. Zomer, 1982. Observations and experiments on the population dynamics of epipelic diatoms from an estuarine mudflat. Estuar. coast. shelf Sci. 14: 471–487.

Amspoker, M. C. & C. D. McIntyre, 1978. Distribution of intertidal diatoms associated with sediments in Yaquina estuary, Oregon. J. Phycol. 14: 387–395.

Anderson, F. E., 1983. The northern muddy intertidal: seasonal factors controlling erosion and deposition – a review. Can. J. Fish. aquat. Sci. 40: 143–159.

Barranguet, C., P. M. J. Herman & J. J. Sinke, 1997. Microphytobenthos biomass and community structure studied by pigment biomarkers: importance and fate in the carbon cycle of a tidal flat. J. Sea Res. 38: 59–70.

Brotas, V., T. Cabrita,, A. Portugal, J. Serodio & F. Catarino, 1995. Spatio-temporal distribution of the microphytobenthic biomass in intertidal flats of Tagus estuary (Portugal). Hydrobiologia 300/301: 93–104.

Cadée, G. C. & J. Hegeman, 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 260–291.

Cadée, G. C.& J. Hegeman, 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balgzand, Dutch Wadden Sea. Neth. J. Sea Res. 11: 24–41.

Coles, S. M. 1977. Benthic microalgal populations on intertidal sediments and their role as precursors to salt marsh development. In Jefferies, R. L. & A. J. Davy (eds), Ecological Processes in Coastal Environments. Blackwell Scientific Publishers, Oxford: 25–42.

Colijn, F. & K. S. Dijkema, 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.

Dade, W. B., J. D. Davis, P. D. Nichols, A. R. M. Nowell, D. Thistle, M. B. Trexler & D. C. White, 1990. Effects of bacterial exopolymer adhesion on the entrainment of sand. Geomicrobiology J. 8: 1–16.

De Jong, D. J. & V. N. De Jonge, 1995. Dynamics and distribution of microphytobenthic chlorophyll-*a* in the Western Scheldt estuary (SW Netherlands). Hydrobiologia 311: 21–30.

De Jonge, V. N., 1985. The occurrence of 'epipsammic' diatom populations: a result of interaction between physical sorting of sediment and certain properties of diatom species. Estuar. coast. shelf Sci. 21: 607–622.

De Jonge, V. N. & J. E. E. Van Beusekom, 1995. Wind- and tide-induced resuspension of sediments and microphytobenthos from tidal flats in the Ems estuary. Limnol. Oceanogr. 40: 766–778.

Delgado, M., V. N. De Jonge & H. Peletier, 1991. Experiments on resuspension of natural microphytobenthos populations. Mar. Biol. 108: 321–328.

De Winder, B., N. Staats, L. J. Stal & D. M. Paterson, 1999. Carbohydrate secretion by phototrophic communities in tidal sediments. J. Sea Res. 42: 131–146.

Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers & F. Smith, 1956. Colorimetric methods for determination of sugars and related substances. Anal. Chem. 28: 350–356.

Frostick, L. E. & I. N. McCave, 1979. Seasonal shifts of sediment within an estuary mediated by algal growth. Estuar. coast. mar. Sci. 9: 569–576.

Grant, J., U. V. Bathmann & E. L. Mills, 1986. The interaction between benthic diatom films and sediment transport. Estuar. coast. shelf Sci. 23: 225–238.

Grant, J. & G. Daborn, 1994. The effects of bioturbation on sediment transport on an intertidal mudflat. Neth. J. Sea Res. 32: 63–72.

Guarini, J.-M., G. F. Blanchard, C. Bacher, P. Gros, P. Riera, P. Richard, D. Gouleau, R. Galois, J. Prou & P.-G. Sauriau, 1998. Dynamics of spatial patterns of microphytobenthic biomass: inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oléron Bay (France). Mar. Ecol. Prog. Ser. 166: 131–141.

Holland, A. F., R. G. Zingmark & J. M. Dean, 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. Mar. Biol. 27: 191–196.

Kornman, B. A. & E. M. G. T. De Deckere, 1998. Temporal variation in sediment erodibility and suspended sediment dynamics in the Dollard estuary. In Black, K.S., D. M. Paterson & A. Cramp (eds), Sedimentary Processes in the Intertidal Zone. Geological Society, London, Special Publications 139: 231–241.

McIntyre, C. D. & W. W. Moore, 1977. Marine littoral diatoms: ecological considerations. In Werner, D. (ed.), The Biology of Diatoms. Blackwell Scientific Publications, Oxford: 333–371.

Montague, C. L., 1986. Influence of biota on erodibility of sediments. In Mehta, A. J. (ed.), Estuarine Cohesive Sediment Dynamics, Lecture Notes on Coastal and Estuarine Studies. Springer-Verlag: 251–269.

Paterson, D. M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnol. Oceanogr. 34: 223–234.

Paterson, D. M., 1997. Biological mediation of sediment erodibility: ecology and physical dynamics. In Burt, N., R. Parker & J. Watts (eds), Cohesive Sediments. Wiley: 215–229.

Pinckney, J. & R. G. Zingmark, 1991. Effects of tidal stage and sun angles on intertidal benthic microalgal productivity. Mar. Ecol. Prog. Ser. 76: 81–89.

Porra, R. J., W. A. Thompson & P. E. Kriedemann, 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorohyll standards by atomic absorption spectroscopy. Biochim. Biophys. Acta 975: 384–394.

Postma, H., 1957. Size frequency distribution of sands in the Dutch Wadden Sea. Arch. Néerl. Zool. 12: 319–349.

Schröder, H. G. J. & F. B. Van Es, 1980. Distribution of bacteria in intertidal sediments of the Ems-Dollard estuary. Neth. J. Sea Res. 14: 268–287.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. Freeman and Company, San Francisco.

Sundbäck, K., 1984. Distribution of microbenthic chlorophyll-*a* and diatoms species related to sediment characteristics. Ophelia 3: 229–246.

Sutherland, T. F., J. Grant & C. L. Amos, 1998. The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on the erodibility of sediment. Limnol. Oceanogr. 43: 65–72.

Underwood, G. J. C., 1997. Microalgal colonization in a saltmarsh restoration scheme. Estuar. coast. shelf Sci. 44: 471–481.

Underwood, G. J. C. & D. M. Paterson, 1993a. Recovery of intertidal benthic diatoms after biocide treatment and associated sediment dynamics. J. mar. Biol. Ass. U.K. 73: 25–45.

Underwood, G. J. C. & D. M. Paterson, 1993b. Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn estuary. J. mar. Biol. Ass. U.K. 73: 871–887.

Underwood, G. J. C. & D. J. Smith, 1998. Predicting epipelic diatom exopolymer concentrations in intertidal sediments from sediment chlorophyll *a*. Microbiol. Ecol. 35: 116–125.

Underwood, G. J. C., D. M. Paterson & R. J. Parkes, 1995. The measurement of microbial carbohydrate exopolymers from intertidal sediments. Limnol. Oceanogr. 40: 1243–1253.

Vos, P. C., P. L. De Boer & R. Misdorp, 1988. Sediment stabilization by benthic diatoms in intertidal sandy shoals; qualitative and quantitative observations. In De Boer, P. L., A. Van Gelder & S. D. Nio (eds), Tide-influenced Sedimentary Environments and Facies. D. Reidel Publishing Company: 511–526.

Watermann, F., H. Hillebrand, G. Gerdes, W. E. Krumbein & U. Sommer, 1999. Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures. Mar. Ecol. Prog. Ser. 187: 77–87.

Wiltshire, K. H., T. Tolhurst, D. M. Paterson, I. Davidson & G. Gust, 1998. Pigment fingerprints as markers of erosion and changes in cohesive sediment surface properties in simulated and natural erosion events. In Black, K. S., D. M. Paterson & A. Cramp (eds), Sedimentary Processes in the Intertidal Zone. Geological Society, London, Special Publications 139: 99–114.