Exopolysaccharide production by marine benthic diatoms
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CHAPTER 3

Spatial patterns of benthic diatoms and carbohydrates on an intertidal mudflat in the Ems-Dollard estuary

Abstract

The chlorophyll $a$ content and two operational fractions of carbohydrate (water extractable and EDTA extractable) were measured along transects on a tidal flat in the Ems-Dollard estuary (The Netherlands). Chlorophyll $a$ was used as a measure 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 contents of chlorophyll $a$ and carbohydrates were low, but in June a high content of up to 90 $\mu$g $g^{-1}$ sediment was found in a narrow zone running parallel to the channel. Maximum contents of water extractable carbohydrate and EDTA extractable carbohydrate ranged between 800-1200 and 600-800 $\mu$g $g^{-1}$ sediment, respectively. The mud content was high (± 90 %) at the margin of the tidal flat, and high diatom densities were only observed in sediment with a high mud content. Alternatively, a high mud content was not limited to the growth season of the diatoms, but was observed throughout the year. This indicated that the high mud content was mainly caused by hydrodynamic factors, and not by biostabilization. June represented a very different situation; the area of high mud content was larger than during the rest of the year, and correlated with high diatom densities. This indicated that the exceptionally high diatom densities in June increased the mud content of the sediment. These observations suggested that mud content and diatom density were interacting variables. The seasonal (June) and spatial (areas of low prevailing erosion rates) restriction of epipelic diatom growth indicated that the influence of accretion by diatoms on sediment mud content was small compared to effects of hydrodynamic factors.
Introduction

On the Heringsplaat, a tidal flat in the Ems-Dollard estuary (The Netherlands) (Fig. 2.1), Kornman & De Deckere (1998) observed that stability of the sediment bed was highest in the period April-June, when the density of benthic diatoms was high. In order to assess the impact of benthic diatoms and exopolysaccharides on biostabilization and sediment transport, more information was 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. Colijn & Dijkema (1981) and Brotas et al. (1995) looked at 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
A description of the study area is given in chapter 2.

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. They were 50 m apart and approximately 250 m long (the approximate location of the transects is indicated in Fig. 3.1). Samples for analysis of carbohydrate, 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
spatial patterns

Fig. 3.1. Dollard estuary indicating the approximate location of transects I to IV on the Heringsplaat (H). Dotted line indicates mean low water mark.

10-20 mm). The triplicate 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 in 1995 and 1996 from 3 or 2 plots of 100 m², 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 m² plots were located close to the transects, and were sampled at monthly intervals. In 1995, sampling was done in triplicate on three plots and only the top cm was used. In 1996, two plots were sampled in triplicate and cores were sectioned into 0-5, 5-10, 10-15 and 15-20 mm slices.

Analyses

Extraction and analysis of carbohydrates and chlorophyll a, and analysis of mud content are described in chapter 2.

Statistical analysis

Level of significance of correlations between variables was analyzed with the Spearman rank correlation coefficient (Sokal & Rohlf, 1981).
Results

A high content of chlorophyll \(a\) (up to 90 \(\mu g\) g\(^{-1}\) sediment) was found in June, whereas in March, October and December chlorophyll \(a\) content was low (less than 10 \(\mu g\) g\(^{-1}\) sediment) (Figs. 3.2a and d). The high chlorophyll \(a\) content in June was observed on all transects, between approximately 50 and 150 m from the channel (only transects I and III are shown; transect I was not sampled in December). Within 50 m from the channel and at distances greater than 150-200 m, chlorophyll \(a\) content fell to less than 20 \(\mu g\) g\(^{-1}\) sediment. The same pattern was observed for the water extractable carbohydrate fraction (Figs. 3.2b and e). EDTA extractable carbohydrate content was also higher in June (up to 800 \(\mu g\) g\(^{-1}\) sediment), but compared with chlorophyll \(a\) or water extractable carbohydrates the differences between June and other sampling periods were less pronounced (Figs. 3.2c and f).

In addition, EDTA extractable carbohydrate content 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 indicated that water extractable carbohydrates were more closely linked to chlorophyll \(a\) than EDTA extractable carbohydrates. When data of water extractable carbohydrates were plotted against chlorophyll \(a\) (Fig. 3.3a), water extractable carbohydrates correlated significantly with chlorophyll \(a\) \((p<0.01; \ r_s=0.21; \ n=161)\). However, when the data from the transect sampled in June were omitted, there was no significant correlation between water extractable carbohydrates and chlorophyll \(a\) \((r_s=0.12; \ n=146)\). The correlation of EDTA extractable carbohydrates with chlorophyll \(a\) was also significant \((p<0.001; \ r_s=0.46; \ n=159)\) (Fig. 3.3b), and remained significant when the data from the June 1996 transect were omitted \((p<0.001; \ r_s=0.45; \ n=143)\).

Chlorophyll \(a\) was almost completely restricted to the top 5 mm of the sediment (Figs. 3.4a and d). Water extractable carbohydrates were also much higher in the top 5 mm than in deeper layers (Figs. 3.4b and e). In contrast, EDTA extractable carbohydrates were found in comparable amounts throughout the top 2 cm of the sediment (Figs. 3.4c and f).

The mud content in the upper sediment layer decreased with increasing distance from the channel (Fig. 3.5). In March, October and December this was a more or less gradual decrease, but in June the pattern was different. At some distance from the channel mud content increased to approximately 90 % and remained high for the next 50-100 m. At increasing distance from the channel mud content decreased to 30-50 % (Fig. 3.5). This pattern was most pronounced along transect III (Fig. 3.5b).

The area of high mud content of the sediment coincided with the area of high
Fig. 3.2. Chlorophyll $a$ (a,d), water extractable carbohydrates (b,c) and EDTA extractable carbohydrates (c,f) in the upper 5 mm along transects I (a,b,c) and III (d,e,f) on 5 March (●), 26 June (▲), 6 October (♦) and 4 December (■) 1996.
Fig. 3.3. Water extractable carbohydrates (a) and EDTA extractable carbohydrates (b) in the upper 5 mm (data from 1995; upper 10 mm) plotted against chlorophyll a. All data (+ and A) and data from June 1996 (△).

chlorophyll a and carbohydrate contents (cf. Figs. 3.2 and 3.5). This was also apparent when chlorophyll a was plotted against mud content (Fig. 3.6): high values of chlorophyll a were found only at high mud values. Alternatively, a broad range of mud content values was observed at low chlorophyll a content. There was no significant correlation between chlorophyll a content and mud content both when the data from the transect from June 1996 were included (r=0.01; n=158) and when these were omitted (r=0.06; n=142).
Fig. 3.4. Chlorophyll $a$ (a,d), water extractable carbohydrates (b,e) and EDTA extractable carbohydrates (c,f) along transects I (a,b,c) and III (d,e,f) at depths of 0-5 mm (○), 5-10 mm (▲) and 10-20 mm (▲) in June 1996.
Fig. 3.5. Mud content of the upper 5 mm along transects I (a) and III (b) on 5 March (●), 26 June (▲), 6 October (✚) and 4 December (■) 1996.

Discussion

In June 1996, contents of chlorophyll $a$ and carbohydrate on the Heringsplaat were much higher than during the rest of the year. Such a seasonal pattern has frequently been observed for microphytobenthos on tidal flats in the Dutch Wadden Sea (Cadée & Hegeman, 1974; Colijn & Dijkema, 1981; Admiraal et al., 1982; chapter 2 this thesis). Also large interannual variations were observed, since chlorophyll $a$ and carbohydrate contents were much higher in 1996 than in 1997 (chapter 2).

Since epipelic diatoms were the only phototrophs in the sediment (Wiltshire
et al., 1998), chlorophyll $a$ could be regarded as a good indication of benthic diatom biomass. The fact that water extractable carbohydrates correlated significantly with chlorophyll $a$ only when the data from the June 1996 transect were included, confirmed that this period represented an exceptional situation. Furthermore, the close coupling of water extractable carbohydrates with chlorophyll $a$ in June 1996 suggested that this fraction consisted of carbohydrates secreted by benthic 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). EDTA extractable carbohydrates also significantly correlated with chlorophyll $a$, suggesting that these carbohydrates were produced by benthic diatoms as well. The fact that EDTA extractable carbohydrate content was 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. These conclusions confirm those derived from seasonal measurements of water and EDTA extractable carbohydrates and chlorophyll $a$ as presented in chapter 2.

Generally, on tidal flats grain size decreases with increasing elevation due to
lower current velocities (Postma, 1957; Coles, 1977). This has been observed for several tidal flats in the Ems-Dollard estuary (Colijn & Dijkema, 1981; Delgado et al., 1991) including the Heringsplaat (Schröder & Van Es, 1980). Contrasting with these findings, we observed an area of high mud content on the margin of the Heringsplaat, which has also been reported for other tidal flats (Postma, 1957; Vos et al., 1988). A high mud content of the sediment found on the edge of a tidal flat in the Wash (England) was 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 contents 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 resuspended 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). Also, Van de Koppel et al. (subm.) demonstrated that epipelic diatoms grow faster 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 was likely, therefore, that diatom growth was controlled by low resuspension rates and/or mud content.

Even though mud content of the sediment was to a large extent independent of chlorophyll a, it seemed that also in this respect the situation in June was very different from the rest of the year. In June the zone of high mud content was broader than during the rest of the year, and this coincided with the zone of high diatom biomass and high carbohydrate content. Apparently, in the area where during the rest of the year mud was removed, in June erosion was prevented by the presence of the diatoms. These observations suggest that there may be an interaction between mud content and diatom growth. Van de Koppel et al. (subm.) suggested a positive feedback mechanism between mud content and diatom growth based on both mathematical modelling and experimental evidence.

Measurements of sediment stability at the margin of the Heringsplaat showed that during the period of high diatom biomass and high carbohydrate content (April-June) sediment stability was higher than during the rest of the year (Kornman & De Deckere, 1998). It should be noted that in areas of high hydrodynamic energy (high erosion rates), i.e. sandy sediments, epipelic diatoms generally do not occur. This means that bio-stabilization by epipelic diatoms is restricted to areas where prevailing erosion rates are low. This suggests that prevention of erosion by diatom exopolysaccharides has only limited consequences for sediment transport. However, it has been shown that epipelic diatoms in inland, sheltered areas of high mud content may enhance the process of salt marsh formation (Coles, 1977; Underwood, 1997). Although erosion rates in these areas are low, bio-stabilization may therefore still affect sediment transport (Underwood & Paterson, 1993a; Underwood, 1997). Similarly, at the margin of the tidal flat bio-stabilization by diatoms may be effective in influencing sediment transport at high diatom densities. It may even be more effective than bio-stabilization in elevated areas, since a large amount of sediment is trapped in a relatively small area, hence the level of accretion per unit diatom biomass may be relatively high.

Concluding, benthic diatoms and exopolysaccharides on the Heringsplaat exhibited a clear seasonal and spatial distribution. Only in early summer (June) diatom concentration and carbohydrate content were high, on the margin of the mudflat in an area of very high mud content. This area of high mud content was also observed when no diatoms were present, and generally mud content was determined by hydrodynamic factors. In early summer the situation was different
since the high concentrations of benthic diatoms resulted in additional accretion of mud. The observations that accretion by diatoms was limited to early summer and to areas where mud content was already relatively high, implied that the influence of diatoms on sediment transport was small compared to the influence of hydrodynamic factors.