The seasonal dynamics of benthic (micro) organisms and extracellular carbohydrates in an intertidal mudflat and their effect on the concentration of suspended sediment

E.M.G.T. de Deckere^{a,*}, B.A. Kornman^{b,**}, N. Staats^c, G.R. Termaat^{b,***}, B. de Winder^{c,***}, L.J. Stal^a & C.H.R. Heip^a

^aNetherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, P.O.box 140, 4400 AC Yerseke, The Netherlands

^bInstitute for Marine and Atmospheric Research Utrecht, Utrecht University, Department of Physical Geography, P.O. Box 80115, 3508 TC Utrecht, The Netherlands

^cLaboratory for Microbiology, ARISE, University of Amsterdam, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands

The Ems-Dollard estuary, situated in the north of the Netherlands near to the German border, is covered for a large part by intertidal flats. Currents and wind- induced waves exert a shear stress on these flats, resulting in resuspension of the sediment. Fluctuations of the suspended sediment concentration in the Dollard are strongly affected by erosion due to wind-induced waves and by settling during calm weather conditions. However it is believed that benthic processes influence the amount of sediment that can be resuspended from the intertidal flats. Therefore suspended sediment concentration above the Heringsplaat, an intertidal flat in the Ems-Dollard estuary, was measured during two seasons and related to the dominant benthic biological features. The benthos and the abiotic sediment characteristics were monitored from 1995 till 1997, at two stations. At both stations a peak of chlorophyll-a concentration was found in spring, caused by a diatom bloom. Meiobenthos was dominated by nematodes, macrobenthos by the polychaete Marenzelleria viridis and the amphipod Corophium volutator.

The seasonal pattern was studied most intensively during 1996. Monthly sampling was done on the Heringsplaat. The flat was covered with ice during March. This period was followed by a clear water phase during spring and an increase of the silt content at the edge of the Heringsplaat. During this period an increase was found of chlorophyll-a concentration and of the carbohydrate concentration. This carbohydrate secretion stabilized the sediment. This finally resulted in a stable diatom mat at the end of the spring and a two-centimeter thick layer of silt. During June a high increase of nematodes and Corophium volutator was found. Nematode density was about 5000 ind per 10 cm² during June and July and Corophium density reached almost 100.000 per m². The diatom population decreased rapidly during June. It is assumed that this is caused by high grazing pressure of the nematodes and of Corophium. The reduced diatom concentration and the increased

^{*} Present address: University of Antwerp, Department of Biology, Universiteitsplein 1, 2610 Wilrijk, Belgium.

[&]quot;Present address: National Institute for Coastal and Marine Management/RIKZ, P.O.Box 9039, 4330 EA Middelburg, The Netherlands.

^{***} Present address: Ministry of Public works, Directic Zeeland, P.O.Box 5014, 4330 KA Middelburg, The Netherlands

bioturbation activity of *Corophium* resulted in reduced sediment stability. The silt content of the sediment surface at the edge of the Heringsplaat reduced and at the same time the turbidity in the water column increased.

KEY WORDS

sediment stability, suspended sediment, macrobenthos, Corophium, Dollard estuary

1. INTRODUCTION

Estuaries are highly dynamic systems that are continuously subject to morphological changes. Erosion, transport and deposition of sediment trigger these changes. Several studies have been carried out in order to understand the physical processes that cause sediment transport and deposition in estuaries (Dyer, 1988; Postma, 1967). Erosion, on the other hand, depends as well on physical processes, induced by waves and currents (De Jonge & van Beusekom, 1995), as on biological processes (Kornman & de Deckere, 1998; Nowell et al., 1981). Organisms living in or on the sediment will alter the sediment properties, which will result in either stabilization or destabilization. Stabilization of the sediment is mainly a result of the excretion of extracellular polysaccharides by diatoms and/or bacteria (Dade et al., 1990; Paterson, 1988). Bioturbation by meio- and macrobenthos results in a destabilization of the sediment by an increase of the water content and/or microtopography (Davis, 1993; de Deckere et al., 2001; Nowell et al., 1981) and indirectly by grazing on stabilizing organisms (Gerdol & Hughes, 1994a).

The Dollard, a part of the Ems-Dollard estuary, consists of intertidal flats for 80 %. These flats are regularly covered with diatom mats, which increase the erosion resistance of the sediment (Kornman & de Deckere, 1998). Meiobenthos consist for almost ninety percent of nematodes, most species found are diatom feeders (Bouwman, 1983). A lot of nematodes are known to build tubes in the surface layers of the sediment (Jensen, 1996), thereby increasing the water content. Protruding tubes will enhance micro turbulence in the boundary layer of the sediment (Eckman et al., 1981). This will be more pronounced by tubes of the amphipod *Corophium volutator*, which is one of the dominant species in the Dollard (Essink et al., 1998). *Corophium* destabilises the sediment directly by changing the microtopography (unpublished results) and indirectly by grazing on diatoms (Gerdol & Hughes, 1994a). *Corophium* can affect the sediment dynamics also by active resuspension of fine sediment particles (de Deckere et al., 2000).

The suspended sediment concentration in the Ems-Dollard estuary is strongly affected by erosion due to wind-induced waves and by settlement during calm weather conditions (De Jonge & van Beusekom, 1995). It is hypothesised that benthic destabilisation and stabilisation processes affect the amount of sediment that can be suspended. Therefore suspended sediment concentration above the Heringsplaat, an intertidal flat in the Ems-Dollard estuary, was measured during two seasons and related to the dominant benthic biological features.

2. MATERIAL AND METHODS

2.1. Study area

The Ems-Dollard estuary is situated in the northeast part of the Dutch Wadden Sea on the border between the Netherlands and Germany (Fig. 1). The Dollard is the upper reach of the estuary, approximately 100 km², and consists for ± 85 % of intertidal flats. The tidal prism of this area is 115 * 10⁶ m³ and the tidal range is 3 m (De Jonge, 1992). Measurements were performed on the Heringsplaat, an ebb dominated mesotidal flat located in the central part of the Dollard (Fig. 1). The sediment at this flat varies between sandy mud and muddy sand. Maximum current velocities during ebb are approximately 0.3 m.s⁻¹. The maximum significant wave height above the flat is

about 0.5 m, due to a combination of the fetch of a few kilometers and the relative shallow water depth (max 1.5 m).

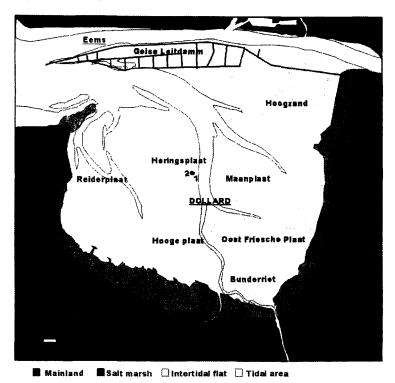


Figure 1. Map of the Dollard estuary with the measuring-bridge situated in the middle on the intertidal flat Heringsplaat (•) and the two sampling stations 1 and 2.

2.2. Sampling

Two plots of 100 m² were monitored from 1995 till 1997. Station 1 was located 100 m from the channel and 100 m south of a huge measuring-bridge (Figure 2)(Kornman & de Deckere, 1998). Station 2 was situated at the higher part of the flat, 250 m from the channel. Sampling was done seasonally during 1995 and with monthly intervals from spring till autumn in 1996 and 1997. Undisturbed cores were taken for chlorophyll-a and carbohydrates (0-5 mm, \emptyset = 1.8 cm, n = 5 (n=number of cores)), grain size (0-5 mm, \emptyset = 3.6 cm, n = 3) and Corophium and nematodes (0-30 cm, \emptyset = 12 cm, n = 3). The samples for chlorophyll-a, carbohydrates and grain size were immediately frozen in the field, samples for benthos were fixed with borax buffered formaldehyde (4%). The suspended sediment concentration in the water column was measured continuously with 3 MEX turbidity sensors during 1996 and 1997 at the bridge (type BTG RD-20/10). The data of the three MEX sensors were averaged and finally an average value was calculated per day. Wind velocity and wind direction were measured at the top of this bridge. The wind velocity data were also averaged per day. The suspended sediment concentrations measured above the Heringsplaat were compared to data measured at the entrance of the Dollard in the main channel "Groote Gat" (Figure 1).

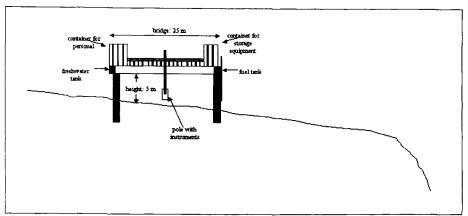


Figure 2. Cross-section of the Heringsplaat and the measuring-bridge

2.3. Analysis

Chlorophyll-a was extracted from freeze-dried sediment (100 mg) by N,N-dimethylformamide. Samples were incubated for 1hour and centrifuged for 5 minutes at 20,000 g. The absorption was measured spectrophotometrically at 665 nm (E_n). Subsequently 15 μ I HCl (5 M) was added to the extract and absorption was measured again (E_a). The chlorophyll-a concentration can then be calculated according to the following equation: chlorophyll-a (g Γ^1) = 2.3 * (E_n - E_a) / 72.114 (de Winder et al., 1999).

Carbohydrates were determined using the phenol-sulfuric acid assay (Dubois et al., 1956). Carbohydrates were extracted from the sediment in two steps. About 200 mg of freeze-dried sediment was extracted with 1 ml of distilled water for 1 hour at 30°C. The sample was centrifuged for 5 min. at 20,000 g. The supernatant contained the colloidal carbohydrates. Subsequently the pellet was extracted for 4 h. by 1.5 ml of a 0.1 M Na₂-EDTA-solution at 20°C. The supernatant contained the EDTA-extractable fraction.

Grain size was analysed with a Malvern Particle Sizer 3600 EC. Corophium and nematodes were counted under a binocular after sieving the sediment respectively over a 500-µm and a 38-µm sieve.

3. RESULTS

Both stations showed an increase of chlorophyll a in spring during 1995 and 1996 (Figure 3a), but contents were higher at station 1, which was situated at the edge of the flat. A pronounced peak of chlorophyll a was observed at this station in the summer of 1996. This coincided with an extensive diatom mat on the surface of the sediment. This mat was not found at station 2 neither during 1995 and 1997 at station 1. Chlorophyll a did not show any seasonal dynamics in the surface layer of the sediment during 1997.

The carbohydrate fractions, the colloidal as well as the EDTA extractable, had higher contents at station 1 than at station 2 till August during 1995 and 1996. The seasonal dynamics of the colloidal and EDTA extractable carbohydrates showed a similar trend as the chlorophyll a dynamics (Figure 3b and 3c). The EDTA extractable fraction showed some differences. An extreme peak was found for this fraction at the beginning of May 1995 and there was not a peak at the end of June 1996. The EDTA extractable carbohydrates remained also higher throughout the winter. A significant relation however was found between chlorophyll a and respectively the colloidal and EDTA extractable

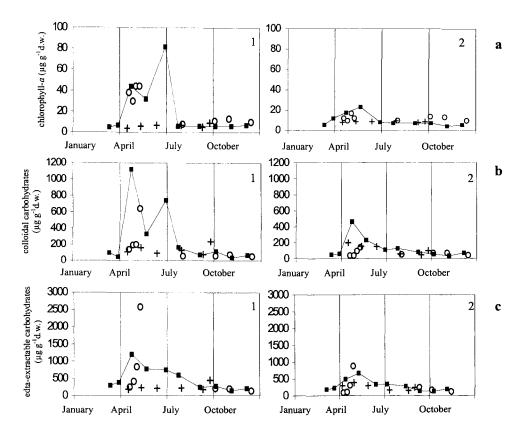


Figure 3. Time series of (a) chlorophyll-a content, (b) colloidal carbohydrate content and (c) EDTA-extractable carbohydrate content, in the upper layer of the sediment (0-0.5cm) at plot 1 (left column) and plot 2 (right column) during 1995(o), 1996(m) and 1997 (+).

fraction of carbohydrates (ANOVA: $F_{18,28} = 4.62$; p < 0.001 and $F_{18,26} = 3.29$; p < 0.01), indicating that the EPS production is strongly affected by the algal community.

The macrofaunal community at the two stations consisted out of 7 up to 12 species (Table 1), no significant difference was found between the plots. In spring the benthos was not dominated by one of the species. Corophium volutator, Hydrobia ulvae, Macoma balthica, Marenzelleria viridis, Nereis diversicolor and oligochaetes were the most common species, but they were far outnumbered by huge densities of Corophium volutator in the summer. The enormous increase of Corophium during the summer was found every year (Figure 4a). Highest density occurred in the beginning of July 1996, namely 82000 ind.m⁻². Density decreased rapidly at station 2, but remained high at station 1. This station was situated in the zone, where a second diatom bloom was observed. Nematodes showed also a peak at the end of June (Figure 4b). Nematode density varied between 400 up to 2300 ind.10 cm⁻², but increased up to 5300 ind.10 cm⁻².

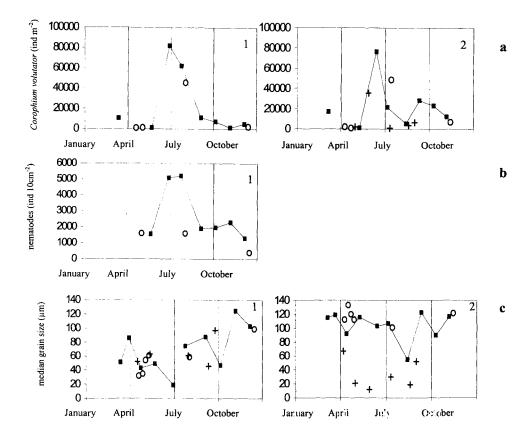


Figure 4. Time series of (a) Corophium volutator density, (b) nematode density and (c) median grain size of the sediment in the upper layer of the sediment (0-0.5cm), at plot 1 (left column) and plot 2 (right column) during 1995(o), 1996(a) and 1997 (+). Nematodes were not sampled in 1997, neither in plot 2.

The sediment at station 1 was sandy silt. The median grain size varied between 20 and 80 μ m in spring (Figure 4c). A decrease was observed from April 1996 to July 1996. A layer of at least two centimeter of fine sediment settled at this site (Figure 5), but this layer eroded during the rest of the summer. Median grain size in the top half centimeter of the sediment increased up to between 50 and 130 μ m. Station 2 was sandier during 1995 and 1996. The median grain size varied around 110 μ m, with a small decrease in the autumn of 1996. Fine sediment settled down at station 2 during the spring of 1997. The median grain size decreased to \pm 20 μ m, and increased slowly during summer.

The suspended sediment concentration in the Dollard showed a similar seasonal trend above the intertidal flat "Heringsplaat" and in the channel "Het Groote Gat", situated at the entrance of the Dollard (Figure 6). The concentration above the intertidal flat was significantly higher. Sediment is eroded here directly by wind waves. The eroded sediment is diluted in the water column, which results in lower concentrations in the channels. Regression analysis showed a low correlation between the daily average wind speed and the daily average suspended sediment concentration

during 1996 ($r^2 = 0.24$). No relation was found at all for 1997. This suggests that besides wind other factors, such as the sediment bed characteristics, are important for the suspended sediment concentration. Analysis of covariance showed that the suspended sediment concentration during 1996 depended both on wind as well as on the dominant biological feature in the sediment ($F_{2, 159} = 0.071$, p < 0.001). Therefore the data of 1996 were divided into three periods, during two of these periods one group of organisms was clearly more abundant and affecting the sediment surface than the other organisms. The first period was characterised by a diatom mat on the surface of the sediment (chlorophyll $a > 20 \mu g.g^{-1}$ d.w. sed.), from 2 April till 19 June. The mat was still present at the end of June, but the abundance of *Corophium volutator* increased enormous. *Corophium volutator* was abundant in high densities (> 25000 ind.m⁻²) at both stations during the second period, which was from 19 June till 9 August. The rest of the year no dominant features were present in the sediment.

Table 1 Macrobenthos density (N.m⁻²) at station 1 and 2 at the Heringsplaat in 1995

Species	Station 1				Station 2			
	19/4	3/5	2/8	14/12	19/4	3/5	2/8	14/12
Arenicola marina							35	
Corophium volutator	580	1275	45647	2293	1971	928	48583	6806
Crangon crangon							35	
Eteona spec.			70				70	50
Heteromastus filiformis	464	696	772	1243	348	116	210	149
Hydrobia ulvae	1044	2087	2210	2238	1044	2667	2771	1492
Hydrobia ventrosa	464	696	491		696	1160	491	
Macoma balthica		1507	1157	497	464	580	456	448
Marenzelleria viridis	2667	2783	1754	1592	2667	3479	3964	2636
Mya arenaria		116	35		116			
Nereis diversicolor	348	812	491	497	1391	464	175	149
Oligochaeta spec.	1623	1507	982	895	580	696	631	647
Pygospio elegans		928	1403		812		1929	

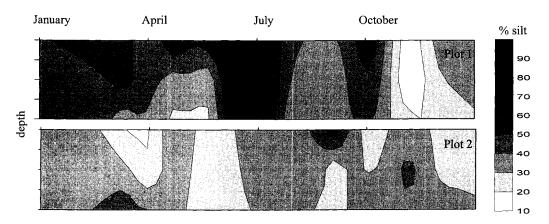


Figure 5. Percentage of silt in the upper two centimeter of the sediment in plot 1 and plot 2 during 1996.

This results in a good relation between the suspended sediment concentration and the wind speed when Corophium density was low and a diatom mat was absent (Figure 7, $r^2 = 0.62$). A good relation was also found for the second period, when Corophium was present at high densities ($r^2 = 0.67$). Suspended sediment concentrations were significantly higher during this period than the other periods. The steepness of the relation, however, was similar to the steepness of the relation for the period when Corophium density was low and a diatom mat was absent. This indicates similar erosion rates in these periods, but an extra input of sediment into the water column when high Corophium densities are present, which cannot be related to the wind speed variability. No significant relation was found between the suspended sediment concentration and the wind speed in the first period, when a diatom mat was present ($r^2 = 0.02$). However the suspended sediment concentrations remained low during this period, clearly indicating a reduced erosion rate.

The results indicate that benthic organisms do have an effect on the amount of sediment that will resuspend when the sediment bed is exposed to wind- and wave stress. The suspended sediment concentration is lower when the tidal flat is covered with a diatom mat binding sediment particles together with mucus, while more sediment will be resuspended when high densities of *Corophium volutator* are abundant.

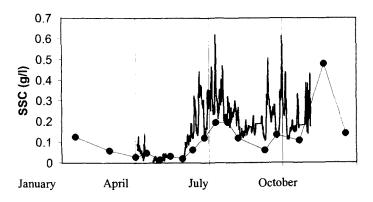


Figure 6. The seasonal variation of the suspended sediment above the Heringsplaat (solid line) and in the channel "Het Groote Gat" (line with dots) during 1996.

4. DISCUSSION AND CONCLUSIONS

The suspended sediment concentration in the Dollard estuary will depend on the wave energy caused by wind as is shown in Figure 7, but benthic processes in the intertidal flats affect the relation. This was most pronounced during 1996, when a diatom mat was formed on the edges of

the Heringsplaat. The suspended sediment concentration remained low as long as the mat was intact, but increased as soon as the abundance of the amphipod *Corophium volutator* started to increase. This coincided with the disappearance of the diatom mat.

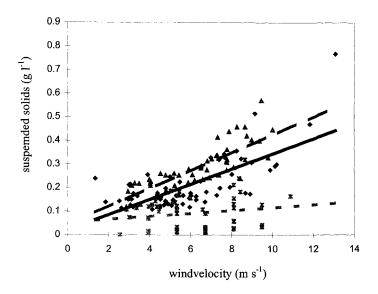


Figure 7. Suspended sediment concentration above the Heringsplaat during 1996 versus the wind velocity. The data were divided over three periods. One period that is dominated by Corophium (Δ), one by diatoms (X) and during the rest of the season (\blacklozenge) no dominating feature was found.

It was observed during the field study that 1996 differed from the other two years. The water column was extremely clear after a severe winter and calm weather (Staats et al., 2001). This resulted in the development of an algal bloom both in the water column and in the sediment. Finally a diatom mat was formed at the end of the spring on the edge of the Heringsplaat (Staats et al., 2001). The dominant diatom species in this mat was largely made up of the genus Nitzschia (Wiltshire et al., 1998). A diatom mat was observed also on the muddier flats at the upper reaches of the Dollard estuary in this period (personal observations). High chlorophyll a contents were found in the spring of 1997 at the upper reaches, but no algal mat was observed (unpublished results). The occurrence of a diatom mat seems to depend on the severity of the winter (Gillbricht, 1964; Staats et al., 2001). The sediment on the intertidal flats seemed to be protected from erosion by the algal mat. The suspended sediment concentration remained low. This was due to an increased shear stress for erosion (Kornman & de Deckere, 1998), which most likely is a result of increased carbohydrate contents of the sediment. These carbohydrates are produced by diatoms and bind sediment particles together. The binding capacity can be ascribed mainly to the EDTAextractable fraction. The colloidal carbohydrates on the other hand will dissolve every time when water covers the flat and will have less effect on the sediment stability. The algal bloom

disappeared during spring, but was followed by a second bloom at the edges of the Heringsplaat. This time a diatom mat was formed. Fine sediment particles were trapped to this mat, thereby increasing the silt content of the sediment. However the increase of silt can also be due to the increase of small *Corophium*, who probably collect fine particles out of the sediment column to build their tubes (Jensen, 1996).

The disappearance of the diatom mat at the end of June is most likely a result of the increased grazing pressure by the increasing number of benthos. A typical estuarine community, such as Corophium volutator, Hydrobia ulvae, Macoma balthica, Nereis diversicolor and oligochaetes, dominates the benthos at the Heringsplaat. Since the early nineties there is also an increase observed of the spionid Marenzelleria viridis. This typical community is to be expected to have a destabilising effect on muddy sediments, thus enhancing erosion of fine sediments at a lower shear stress (de Deckere et al., 2001). Destabilisation occurs directly by an increase of the microtopography, thereby enhancing microturbulence resulting in an increased shear stress (Eckman & Nowell, 1984). Indirect destabilisation is due to grazing and reduction of microphytobenthos. Microphytobenthos is known to stabilise the sediment by secretion of carbohydrates. On the other hand the benthos can enhance the amount of suspended material by ejecting sediment particles into the water column (de Deckere et al., 2000). The secretion of faecel pellets, which will erode more easily, was also observed in the field for Marenzelleria. The erosion of faecal pellets can also strongly effect the erosion rate. This was shown for the faecel pellets of Hydrobia ulvae at two microtidal mudflats in the Danish Wadden Sea (Andersen, 2001).

Benthic diatoms form a significant part of the diet of *Corophium volutator* (Creach et al., 1997; Gerdol & Hughes, 1994b). They can selectively pick out diatoms, but they can also feed on bacteria or organic films, like colloidal or EDTA-extractable carbohydrates. An ingestion rate of 1.5 ng chl ind h⁻¹ h⁻¹ was found in laboratory experiments (Gerdol & Hughes, 1994b). This was equivalent to approximately 4000 small diatoms. Considering the density of *Corophium* of ± 80000 ind m⁻² at the end of June, a grazing pressure of 120 μg chl m⁻² h⁻¹ could be expected. However this grazing rate will be an overestimate, because *Corophium* were starved before the experiment started. At the same time an increase was reported for nematodes. Nematodes were the most abundant meiobenthic species in the Heringsplaat. Up to 90% of the species found in the Dollard estuary are categorised as diatom feeding species (Bouwman, 1983; Riemann & Schrage, 1978). Feeding rates found for nematodes vary between 40 diatoms per day up to 7 diatoms per hour (Admiraal et al., 1983). This means a daily consumption of approximately 10 ng C ind d⁻¹. Blanchard (1991) found similar rates, but, contrary to the previous author, he concluded that nematodes could become food limited because of high grazing pressure. Despite the inaccuracy of the reported grazing rates, it seems likely that the diatom mat collapsed during July due to the high grazing pressure by the benthos.

The resuspension of both sandy as well as muddy sediments in estuaries can be strongly related to the wind-induced waves (De Jonge & van Beusekom, 1995; Freire & Andrade, 1999). Our results show that benthic processes affect this relation. The clear water phase in spring was most likely not a result of this, but consequently a diatom bloom at the intertidal areas restricted the resuspension of the sediment. This confirms the hypothesis that diatoms stabilise the sediment by mucus secretion (Paterson, 1989). The increased suspended sediment concentration in the summer confirmed both the direct as well as the indirect effect of the benthic population. The indirect effect by grazing on the diatoms showed a decrease of the sediment stability, but the direct effect seemed much more related to a direct input of suspended sediment into the water column than reduced sediment stability.

The results of this study demonstrate clearly the impact of benthic organisms, both of microphytobenthos and of macrobenthos, on the suspended solids concentration. The relation is not straightforward and will also depend on climatic and hydraulic conditions, but the effect can clearly be distinguished in the field. Therefore it is recommended to include information about benthic

organisms when studying the behaviour of sediments in tidal areas, especially for the prediction of resuspension.

ACKNOWLEDGEMENTS

The authors wish to thank the crew of the R.V. "NAVICULA" and Willem van der Lee, skipper of the R.V. "GEOS". 'Meetdienst Noord' of the Ministry of Transport, Public Works and Water Management provided the data of the "Groote Gat". This study was financially supported by the Dutch organisation NWO-GOA as a part of the BOA research theme on tidal areas and by the European Community grants MAS3-CT95-0022 INTRMUD. This is publication 2812 of the Netherlands Institute of Ecology, Centre of Estuarine and Coastal Ecology, Yerseke.

REFERENCES

- Admiraal, W., L.A. Bouwman, L. Hoekstra, & K. Romeyn, 1983, Qualitative and quantitative interactions between microphytobenthos and herbivorous meiofauna on a brackish intertidal mudflat, *Internationale Revue der gesamten Hydrobiologie.*, (68), 175-191.
- Andersen, T.J., 2001, Seasonal variation in erodibility of two temperate, microtidal mudflats, Estuarine, Coastal and Shelf Science, (53), 1-12.
- Blanchard, G.F., 1991, Measurement of meiofauna grazing rates on microphytobenthos: is primary production a limiting factor?, *Journal of experimental Marine Biology and Ecology*, (147), 37-46.
- Bouwman, L.A., 1983, Systematics, ecology and feeding biology of estuarine nematodes, BOEDE Publications and reports 3, Ph.D.-thesis, Agricultural University, Wageningen, 173 p.
- Creach, V., M.T. Schricke, G. Bertru, & A. Mariotti, 1997, Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers, *Estuarine*, *Coastal and Shelf Science*, (44), 599-611.
- 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, *Geomicrobiological Journal*, (8), 1-16.
- Davis, W.R., 1993, The role of bioturbation in sediment resuspension and its interaction with physical shearing, *Journal of experimental Marine Biology and Ecology*, (171), 187-200.
- de Deckere, E.M.G.T., T.J. Tolhurst & J.F.C. de Brouwer, 2001, Destabilisation of muddy intertidal sediments by benthos, *Estuarine, Coastal and Shelf Science*, (53), 665-669.
- de Deckere, E.M.G.T., J. van de Koppel, & C.H.R. Heip, 2000, The influence of *Corophium volutator* abundance on resuspension, *Hydrobiologia*, (426), 37-42.
- De Jonge, V.N., 1992, Physical processes and dynamics of microphytobenthos in the Ems estuary (The Netherlands), Ph.D.-thesis, University of Groningen, 176 p.
- De Jonge, V.N. & J.E.E. van Beusekom, 1995, Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary, *Limnology &Oceanography*, (40), 766-778.
- de Winder, B., N. Staats, L.J. Stal, & D.M. Paterson, 1999, Carbohydrate secretion by phototrophic communities in tidal sediments, *Journal of Sea Research*, (42), 131-146.
- Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers, & F. Smith, 1956, Colorimetric method for determination of sugars and related substances, *Analytical Chemistry*, (28), 350-356.
- Dyer, K.R., 1988, Fine sediment particle transport in estuaries. In Dronkers, J. (ed.), *Physical processes in estuaries*, Springer-Verlag, Berlin: 295-310.
- Eckman, J.E. & A.R.M. Nowell, 1984, Boundary skin friction and sediment transport about an animal-tube mimic, *Sedimentology*, (31), 851-862.

- Eckman, J.E., A.R.M. Nowell, & P.A. Jumars, 1981, Sediment destabilization by animal tubes, Journal of Marine Research, (39), 361-374.
- Essink, K., J. Eppinga, & R. Dekker, 1998, Long-term changes (1977-1994) in intertidal macrozoobenthos of the Dollard (Ems Estuary) and effects of introduction of the North American spionid polychaete *Marenzelleria* cf. wireni, Senckenbergiana Maritima, (28), 211-225.
- Freire, P. & C. Andrade, 1999, Wind-induced sand transport in Tagus estuarine beaches, *Aquatic Ecology*, (33), 225-233.
- Gerdol, V. & R.G. Hughes, 1994a, Effect of Corophium volutator on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England, *Marine Ecology Progress Series*, (114), 109-115.
- Gerdol, V. & R.G. Hughes, 1994b, Feeding behaviour and diet of Corophium volutator in an estuary in southeastern England, *Marine Ecology Progress Series*, (114), 103-108.
- Gillbricht, M., 1964, Einwirkungen des kalten Winters 1962/63 auf die Phytoplanktonwicklung bei Helgoland, *Helgoländer Meeresuntersuchungen*, (10), 263-275.
- Jensen, P., 1996, Burrows of marine nematodes as centres for microbial growth, *Nematologica*, (42), 320-329.
- Komman, 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., D.M. Paterson, & A. Cramp (eds), Sedimentary Processes in the Intertidal Zone, Geological Society, London, Special Publications, 139: 231-241.
- Nowell, A.R.M., P.A. Jumars, & J.E. Eckman, 1981, Effects of biological activity on the entrainment of marine sediments, *Marine Geology*, (42), 133-153.
- Paterson, D.M., 1988, The influence of epipelic diatoms on the erodibility of an artificial sediment, Proceedings of the 10th Diatom Symposium, 345-355.
- Paterson, D.M., 1989, Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms, *Limnology & Oceanography*, (34), 223-234.
- Postma, H., 1967, Sediment transport and sedimentation in the estuarine environment. In Lauff, G. H. (ed.), *Estuaries*, American Association of Advanced Scientific Publications, 158-184.
- Riemann, F. & M. Schrage, 1978, The mucus-trap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture, *Oecologia*, (34), 75-88.
- Staats, N., E.M.G.T. de Deckere, B. de Winder & L.J. Stal, 2001, Spatial patterns of benthic diatoms, carbohydrates and mud on a tidal flat in the Ems-Dollard estuary, *Hydrobiologia*, (448), 107-115.
- Staats, N., E.M.G.T. de Deckere, B.A. Kornman, W. van der Lee, R. Termaat, J. Terwindt & B. de Winder, 2001, Observations on suspended particulate matter (SPM) and microalgae in the Dollard estuary, The Netherlands: importance of late winter ice cover of the intertidal mudflats, *Estuarine, Coastal and Shelf Science*, (53), 297-306.
- Wiltshire, K.H., T.J. 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, 99-114.