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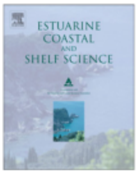

Erodibility of a mixed mudflat dominated by microphytobenthos and *Cerastoderma edule*, East Frisian Wadden Sea, Germany

T.J. Andersen [a,b,*], M. Lanuru [a,c,d], C. van Bernem [a], M. Pejrup [b], R. Riethmueller [a]

[a] *Institute of Coastal Research, GKSS Research Centre, Max Planck Str., 21502 Geesthacht, Germany*
[b] *Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark*
[c] *Coastal Research Laboratory, Institute of Geoscience, Kiel University, Otto-Hahn Platz 3, 24118 Kiel, Germany*
[d] *Department of Marine Science, Hasanuddin University, Makassar 90245, Indonesia*

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ABSTRACT

Sediment erodibility and a range of physical and biological parameters were measured at an intertidal site in the German Wadden Sea area in June, September and November 2002 and February and April 2003 in order to examine the influence of macrozoobenthos and microphytobenthos on sediment erodibility and the temporal variation. The study site was a mixed mudflat situated in the mesotidal Baltrum–Langeoog tidal basin at the East Frisian barrier coast. The mud content at the site was about 35% and the filter-feeding cockle *Cerastoderma edule* was the dominating macrozoobenthic species (by biomass). The erodibility of the sediment showed strong temporal variation with high erosion thresholds in spring and late summer and significantly lower thresholds during the rest of the study period. The erosion thresholds were strongly dependent on the contents of chlorophyll *a* (chl *a*) and colloidal carbohydrates, both indicators of the content of microphytobenthos, in this environment primarily benthic diatoms. The content of microphytobenthos was high in September 2002 and April 2003, and regression analysis indicated that this was the only likely reason for the low erodibility found at these times. A biostabilisation index of about 4.5 was found for a situation with both abundant biofilms and cockles.

A direct influence of *Cerastoderma edule* on erodibility was not observed, in contrast to other recent studies. The presence of *C. edule* at the site results in biodeposition of fine-grained material and the presence of *C. edule* will therefore probably increase the content of fine-grained sediments at the surface compared to an abiotic situation. Increasing the amount of fine-grained material in mixed sediments has previously been shown to reduce the erodibility of the sediments and *C. edule* will therefore in this way indirectly stabilize the bed. However, although *C. edule* may constitute the main part of the biomass at some intertidal sites, other and more vigorous bioturbators and deposit-feeding species (e.g., the bivalve *Macoma balthica*, the gastropod *Hydrobia ulvae* or the amphipod *Corophium volutator*) may completely hide its effect on sediment erodibility if these species are present in high numbers.

1. Introduction

The results of an increasing number of studies dealing with the erodibility of fine-grained intertidal deposits have been published in recent years. There has been a general shift towards studies *in situ* as opposed to laboratory studies on settled sediment beds which rarely reflect the complexity of the interactions between biology, sediment and hydrodynamics as it is found in the field. A large number of the studies *in situ* have shown that the erodibility (mostly expressed as the critical bed shear stress for erosion, the erosion threshold, but sometimes also as erosion rate) was highly influenced by biotic processes. Especially the ability of benthic diatoms to increase the erosion threshold has received much attention and is well documented (e.g. Paterson, 1989; Paterson et al., 1990; Yallop et al., 1994; Sutherland et al., 1998a,b; Lanuru et al., 2007). The diatoms produce extracellular polymeric substances (EPS) during locomotion and this will, when diatoms are present in high densities, increase the erosion threshold because the mucus will create bonds between the bed-particles (Paterson, 1997). Due to the strong temporal and spatial variability of the stock of benthic diatoms, large spatial and temporal variations in the erodibility of intertidal mudflats have been reported

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* Corresponding author at: Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark.
E-mail address: tja@geo.ku.dk (T.J. Andersen).

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(Underwood and Paterson, 1993; Widdows et al., 2000a,b; Andersen, 2001; Herman et al., 2001; Defew et al., 2002; Tolhurst et al., 2006). An additional source for variation in erodibility is temporal variation in production of carbohydrates by diatoms which was reported by Sutherland et al. (1998a,b).

Macrozoobenthos may also affect the erodibility of fine-grained sediments; both directly due to bioturbation and pelletisation of the bed and indirectly due to grazing on diatoms (Nowell et al., 1981; Widdows et al., 1998; Austen et al., 1999). However, quantitative *in situ* studies on the effect of macrozoobenthos on erodibility have only been undertaken on a limited number of species (see review by Widdows and Brinsley, 2002). Both the infaunal bivalve *Macoma balthica* (Widdows et al., 1998, 2000b) and the small epibenthic mudsnail *Hydrobia ulvae* (Blanchard et al., 1997; Andersen, 2001; Andersen et al., 2002, 2005) have been shown to increase the erodibility of fine-grained deposits; both due to pelletisation and grazing activities. Also the amphipod *Corophium volutator* has been shown to affect the erodibility, primarily due to its grazing on diatoms (Gerdol and Hughes, 1994; Grant and Daborn, 1994; de Deckere et al., 2000, 2002) but also its bed-forming activities (Mouritsen et al., 1998).

The filter-feeding bivalve *Cerastoderma edule*, the common cockle, is a widespread and often dominating species with respect to biomass in the European Wadden Sea area (Beukema, 1976) and some studies were specifically aimed at a determination of this species effect on erodibility of fine-grained sediment (Widdows et al., 1998; Ciutat et al., 2006, 2007; Neumeier et al., 2006). Only the studies by Widdows et al. (1998) were carried out without manipulation of the sediment and/or the animal densities. Ciutat et al. (2006, 2007) and Neumeier et al. (2006) found an increase in sediment erodibility with increasing density of the cockle in laboratory studies. Widdows et al. (1998) also reported some effect of the presence of *C. edule* on sediment erodibility but the density of the cockle was quite low at the study site and any direct effect was probably overridden by the effect of the much more numerous bivalve *Macoma balthica*. In summary, the studies generally showed increased erodibility when cockles were present and this increase was explained as a result of increased bed roughness (Neumeier et al., 2006) and bioturbation (Ciutat et al., 2006, 2007). A substantial contribution to the apparent increase in erodibility found in laboratory studies is erosion of faeces and pseudo-faeces (Neumeier et al., 2006). Erosion of these bioaggregates generates no net-erosion of the bed (they are deposited by the cockles themselves) and therefore, the observed increase in erodibility does not necessarily give a true picture of the net-effect of the cockles in nature. It is also likely that cockles manipulated in the laboratory will show increased mobility and hence bioturbation of the sediment. For these reasons the net-effect of cockles with respect to sediment erodibility may be overestimated in laboratory studies. The present study therefore aims at a determination *in situ* of the net-effect of cockles with respect to stability of a tidal flat which showed a commonly observed variation, both seasonally and spatially, of cockles and microphytobenthos. The results will be discussed in relation to laboratory studies on the effect of both cockles, microphytobenthos and mud content.

2. Study site

The studied mixed mudflat is situated on “Dornumer Nacken” in the tidal basin behind the barrier islands Baltrum and Langeoog in the East Frisian part of the German Wadden Sea Area in the southern North Sea (Fig. 1). The basin is mesotidal with a tidal range of approximately 2.6 m. The texture of the deposited sediments in the basin has been described by Krögel and Flemming (1998) and the basin consists largely of intertidal sand flats and mixed mudflats. The salt marshes in the area have been diked and only a narrow band of salt marsh is present in front of the dikes. Low breakwaters inundated only at high-water are situated 200 and 400 m in front of the dikes in order to increase the sediment accumulation. *Cerastoderma edule* can be found in typical densities of 50–300 ind. m^{-2} in the area (van Bernem, unpublished data) although densities of adults up to 3000 ind. m^{-2} were reported by Linke (1939) for the tidal flats in the nearby Jadebusen tidal basin. The climate at the site is temperate and measurements of water temperature from a pile in the basin showed a maximum in August with average temperatures of about 23 °C whereas the average daily temperature often drops below zero in the period December–March. The winter 2002–2003 was slightly colder than average with partial ice-coverage of the basin in some of the period December–February.

The erodibility of the tidal flat sediments at a number of sites in the area has been studied by Lanuru et al. (2007) and the present study focuses on the temporal variation of erodibility of the surface sediments at one particular site situated approximately 900 m from the mainland dike and characterized by a mud content (fraction finer than 63 μm) of 30–40% and dominated by *Cerastoderma edule* and microphytobenthos. The average inundation period during each tidal cycle is 7 h during calm weather conditions and maximum tidal current velocities are about 25 cm s^{-1}. A hummocky surface was found in June with alternating crests and pools of a horizontal scale of about 1 m and heights of up to about 5 cm. The crests were lower in September and November (max about 2 cm) and bedforms were absent in February and April 2003. There are no published studies on the present accumulation rate of sediments at the site but preliminary investigations using ^{210}Pb-dating indicates a recent accumulation rate in the order of 7 mm y^{-1} (T.J. Andersen, unpublished data).

3. Methods

The site was visited in June, September and November in 2002 and in February and April 2003 and between 10 and 12 erosion experiments were carried out during each visit. The experiments were done in pairs (one on a crest and one in a trough) and conducted along a transect with a spacing of approximately 10 m between each pair. The transect, 50 m long, was situated perpendicular to a small gully with the first station on the levee of the gully. Bedforms were not present in February 2003 and in this case only 7 erosion experiments were carried out 20–30 m from the gully.

3.1. Bed samples

A surface scrape of the topmost 1 mm of the bed was analysed for grain-size distribution, fecal pellet content, organic content, content of chl *a*, water extractable colloidal carbohydrate and extracellular polymeric substances (EPS). Analyses of carbohydrates were only carried out in June and September. Additional samples of the topmost 5 mm of the bed were taken with a syringe (diameter 21 mm, five samples pooled into one sample) and analysed for dry bulk density.

Grain-size analyses were carried out by use of a Malvern Mastersizer/E laser-sizer after careful dispersion in 0.01 M $Na_2P_4O_7$ and ultrasonic treatment for 3 min prior to analysis. Fecal pellets originating from the polychaete *Heteromastus filiformis* were abundant at the site and the pellet contents of the bed material and calibration samples for the OBS-sensor were determined by gentle wet-sieving of a sub-sample at 63 μm and examination of the retained material under microscope in order to estimate the fecal pellet content in this material. The retained material was

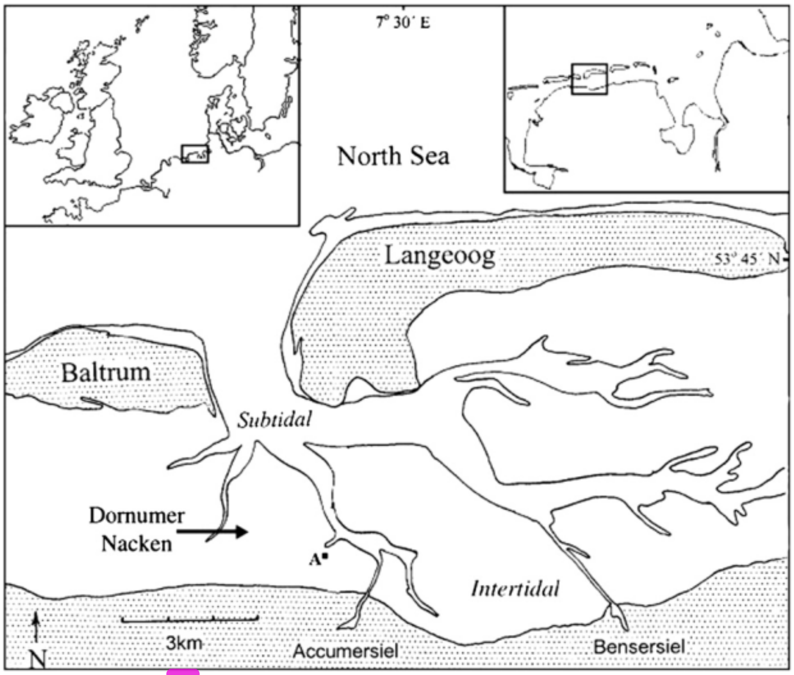

Fig. 1. Map of the study area with the station marked with an "A".

subsequently given an ultrasonic treatment for 2 min and wet-sieved at 63 µm again in order to separate fecal pellet material and sand and shell-fragments. Organic contents were determined by loss on ignition (LOI) after combustion for 2 h at 550 °C.

Chl *a* contents were determined after extraction in 90% acetone by high performance liquid chromatography (HPLC, Wright et al., 1991) in June, September, February and April and by spectrometry in November.

The contents of colloidal (water extractable) carbohydrate and EPS were quantified using the phenol-sulphuric spectrometric assay (Dubois et al., 1956). 5 ml of 25 ppt saline water was added to 100–150 mg sediment. The sample was left for 15 min followed by centrifugation for 15 min at 2500 rpm. 1 ml of the supernatant was used for the determination of the colloidal fraction. The more tightly bound carbohydrate fraction EPS was found by adding 7 ml ethanol to 3 ml of the extract. The sample was stored at 5 °C overnight followed by centrifugation for 15 min at 2500 rpm. The pellet was subsequently resuspended in 1 ml distilled water.

The sediment from each erosion core (area = 0.0079 m^2) was sieved at 1 mm and the macrozoobenthos were described and counted. The density of *Cerastoderma edule* in the area was also determined for plots of 0.25 m^2 because the true density of the cockle would be underestimated if calculated on the core-data alone. This is due to the fact that when cockles were present at or close to the edge of the cores, the sediment surface would often crack and the cores would be discarded for erosion experiments.

3.2. Erosion experiments

The erosion experiments were carried out using a portable EROMES erosion equipment. The equipment was originally described by Schünemann and Kühl (1991) and the portable version and its calibration were described in detail by Andersen (2001). Four additional experiments in June and September were carried out using the original lab-version of the same instrument where undisturbed sediment cores are brought ashore and analysed in the laboratory. Basically, the erosion instrument consists of a 100 mm diameter perspex tube that is pushed into the undisturbed bed sediment. The tube is gently filled with local seawater and the eroding unit is placed on top of the tube. This eroding unit consists of a propeller that generates a primarily tangential flow and hence bed shear stresses and an OBS-sensor, which monitors the changing suspended sediment concentration (SSC). The propeller revolutions are transferred to bed shear stress by use of a calibration based on the onset of erosion of quartz sands with known critical erosion shear stress (Schünemann and Kühl, 1991). Additionally, the bed shear stress has been measured directly by use of a hot-film probe at different radii within the instrument (Andersen, 2001).

During each erosion experiment, the bed shear stress was increased in steps of 0.1 N m^{-2} every 2 min from 0.1 N m^{-2} to 1.0 or 1.5 N m^{-2} (depending on the erosion threshold of the bed). The bed shear stress was maintained for 5 min at 0.5 and 1.0 N m^{-2} in order to reach a situation with close to zero erosion rate. The erosion rates, which are reported here, are the average erosion rates during the application of the bed shear stresses between 0.5 and 1.0 N m^{-2}. The erosion thresholds were determined by use of plots of erosion rates versus applied bed stress. A linear fit was made through the data points in the region of the onset of erosion and the threshold was determined as the bed shear stress at the intercept of this line with a critical erosion rate; the erosion rate above which significant erosion of the sediment surface starts to take place. A critical erosion rate of 0.01 g m^{-2} s^{-1} was used which corresponds to the erosion of the least stable material at the surface (e.g., low-density flocs and bioaggregates). Samples for the calibration of the OBS-sensor were withdrawn from the instrument during each experiment and filtered through pre-weighed Millipore 0.45 µm CEM filters. The sediment on some of the Millipore filters was later analysed for grain-size and fecal pellet content.

The aggregation and settling velocity of the eroded material were analysed as part of the erosion experiments by monitoring the change in SSC as the propeller was turned off after the 0.5 N m^{-2} step and the suspended material was allowed to settle. The erosion experiments continued to 1.0 and 1.5 N m^{-2} after these settling experiments. In order to make the data directly comparable (compensate for the changing viscosity of the water with changing temperature), the settling velocities were converted to equivalent settling diameters (ESD) by use of Stokes' law. The equivalent settling diameter is the diameter of an imaginary spherical quartz grain that settles at the same speed as the aggregate in question. The actual diameter of the aggregate is larger, often much larger, due to the lower density and irregular shape of the aggregate. Stokeś law is only strictly applicable for grains/aggregates in the silt and clay range but only minor errors are found up to a Reynolds number of about 5 (Eisma, 1993). This corresponds to an equivalent grain-size of about 200 µm at 10 °C, which is about twice as large as the largest grains in suspension during the settling experiments of this study.

3.3. Bed-level changes

Changes in the bed-level between September and November (2002) and February (2003) were determined by measurements to 5 stainless steel metal plates (25 * 25 cm) which were buried at distances of 3, 15, 35, 70 and 100 m from the gully. The plates were pushed horizontally into the walls of small holes which were dug into the bed and subsequently carefully filled with sediment. This procedure ensures that they are installed beneath undisturbed sediment and the surface of the disturbed sediment surface next to the plates generally returns to a natural pre-disturbance state within a few weeks after which the measurements can begin. The distance from the surface to the metal plates was determined at 5 places for each plate during each visit and the accuracy of this method is ±2 mm. In February 2003 only four plates were found, the marking-stick for the 70 m plate was removed by ice during the winter.

4. Results

The surface sediments at the site were a mixture of very fine-grained sand and mud and the grain-size distributions of the bed material were bi-modal and showed that the surface material consisted of well-sorted sand with an average grain-size of about 105 µm and poorly sorted silt and clay with a mode at about 15 µm. The mud content of the surface material was about 35% and showed no significant temporal variation but a decrease with depth was observed, reaching about 15% mud at 20 cm depth. Grain-size analyses were also carried out on disaggregated pellets from *Heteromastus filiformis* and the texture of the pellets was significantly finer with a mud content of about 77%.

The average densities of the main macrozoobenthic species are given in Table 1. The macrozoobenthic community was dominated by *Cerastoderma edule* and *Heteromastus filiformis*. The density of *C. edule* was within the range generally observed in the Wadden Sea (e.g., Linke, 1939; Beukema, 1976; Smaal et al., 1986; Jensen, 1992). The density of *H. filiformis* (4000 ind. m^{-2}) was within the range Linke (1939) considered high (2000–4000 ind. m^{-2}). There was no significant temporal change in the density of *C. edule* when calculated from the erosion core-data and the density presented in Table 1 is the one based on plots of 50*50 cm. *Hydrobia ulvae* was only present in November and February (average: 837 ind. m^{-2}).

Table 1
The main macrozoobenthic species present at the study site. Average from all the investigation periods.

Species	Ind. m^{-2}
Cerastoderma edule	184
Macoma balthica	88
Hydrobia ulvae	0–837
Nereis diversicolor	400
Heteromastus filiformis	3400

The bed-level decreased both in the period September–November (average −1.9 cm ± 0.3 cm, *n* (number of plates) = 4) and November–February (−1.0 cm ± 0.1 cm, *n* = 3). The station closest to the gully showed larger erosion in the period September–November (−4.3 cm) and slight deposition in the period November–February (+0.3 cm).

The erosion thresholds for the sediments generally varied between 0.2 and 0.6 N m^{-2} but significantly higher thresholds (up to 1.8 N m^{-2}) were observed in September and April (*t*-test, $P = 0.007$). Similarly, significantly higher contents of chl *a* were observed in September and April and lower contents in the rest of the study period (*t*-test, $P < 0.001$). A comparison of the average SPM-data from the experiments in September 2002 and February 2003 is shown in Fig. 2. A plot of the temporal variation of the chl *a* content and erosion threshold is shown in Fig. 3. Colloidal carbohydrates and EPS were only measured in June and September and much larger values were observed in September (*t*-test, $P < 0.001$). The average erosion rate for the steps 0.5–1.0 N m^{-2} showed a maximum of 0.00033 kg m^{-2} s^{-1} and was generally below 0.0002 kg m^{-2} s^{-1}. This is about a factor five lower than the rates reported by Andersen (2001) using the same instrument for a mudflat dominated by *Hydrobia ulvae*. The erosion rates showed opposite trends compared with the erosion thresholds due to the close link between the two. As a result, analysis of the variability in erosion rates did not reveal any variations in erodibility which could not be ascribed to variations in erosion thresholds, and therefore the erosion rates are not discussed further in this paper.

Small-scale variations in the abundance of *Cerastoderma edule* were observed and the number of individuals in the erosion cores ranged from 0 to 5 corresponding to densities from 0 to 635 ind. m^{-2}. Fecal pellets from *Heteromastus filiformis* were found in all samples and were between 8 and 24% by weight. The dry bulk density of the sediment varied between 0.69 and 1.12 g cm^{-3} and

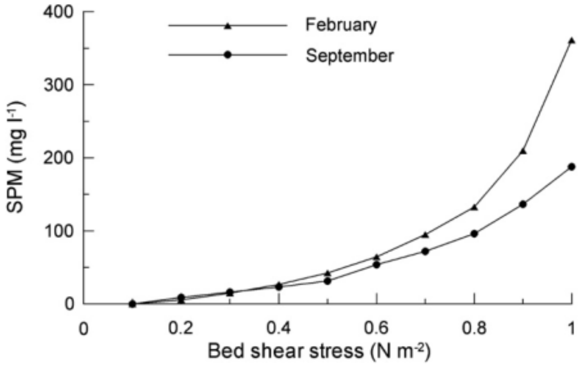

Fig. 2. The average variation of SPM in the erosion experiments in September 2002 and February 2003.

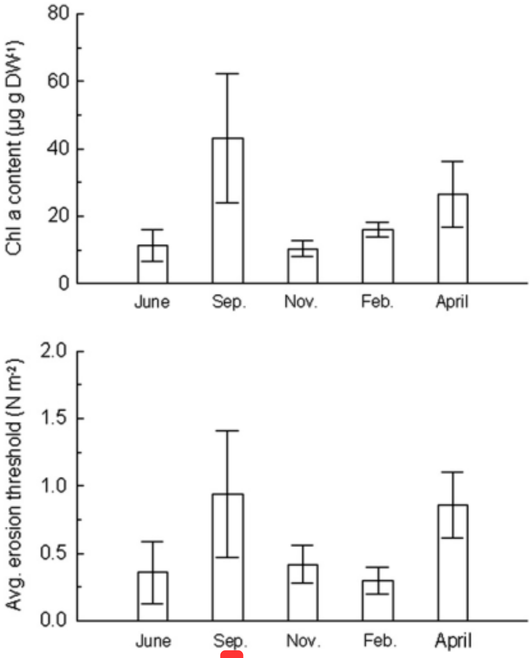

Fig. 3. The temporal variation of the content of chl *a* and the average erosion threshold for each of the field campaigns. Average of 6–12 experiments ± STD.

organic content between 1.3 and 3.6%. Neither macrofauna densities, dry bulk density, fecal pellet content or organic content showed significant temporal variations.

There was no systematic spatial variation within the area for any of the measured parameters with respect to distance from the gully. Occasionally differences were observed with respect to the vertical position (position on crests or in troughs). No significant differences were observed in June but the chl *a* contents were higher on crests than in troughs in September (*t*-test; $P = 0.01$). In November, erosion thresholds were higher on crests than in troughs (*t*-test; $P = 0.04$). Bedforms were absent in February and April 2003.

Linear regression analysis has been conducted between the main measured parameters and the correlation coefficients are presented in Table 2. Numbers in bold indicate highly significant correlations ($P < 0.01$). Only very limited variation was observed with respect to sand content, fecal pellet content, organic content and dry bulk density at the site, and consequently these parameters generally showed low correlation with erosion threshold and erosion rate. In contrast, the contents of chl *a*, colloidal carbohydrates and EPS were strongly co-varying and showed significant correlation with the erodibility at the site. The erosion thresholds were especially well correlated to these three parameters and plots of the erosion thresholds versus the contents of chl *a*, colloidal carbohydrates and EPS are shown in Figs. 4–6 respectively. In the order of 80% of the variance in the erosion thresholds can be explained by these indirect measures of microphytobenthic stock. The data from the portable and the lab-version of the EROMES are plotted separately in these figures. However, a test of the influence of erosion-method using a multiple linear regression showed no significant difference and results from the two data-sets are treated as one data-set in the following.

There was no correlation between the erodibility of individual sediment cores and the density of the cockles in the cores (Fig. 7).

A biostabilisation index S_b (e.g. Tolhurst et al., 1999) can be calculated as the ratio of the erosion thresholds with and without biological influence. If the hypothetical (and unrealistic) case of complete absence of colloidal carbohydrates and/or EPS is considered, an expected erosion threshold of about 0.2 $N\,m^{-2}$ can be found based on the linear fits in Figs. 5 and 6. Using this value as a best estimate of the erosion threshold at abiotic conditions a stabilisation index of 4.7 is found in September and 4.3 in April.

For the experiments in November, analyses of the eroded material for content of fecal pellets and grain-size distributions have been undertaken. Both sand and fecal pellets from *Heteromastus filiformis* were virtually absent in the suspended material at a bed shear stress of 0.5 $N\,m^{-2}$ but the content of fecal pellets in suspension did not differ significantly from the bed material at 1.0 $N\,m^{-2}$. The content of sand in suspension was still lower than the bed material at 1.0 $N\,m^{-2}$ (50% compared to 64%, *t*-test; $P < 0.001$) but the contents were similar at 1.5 $N\,m^{-2}$ (*t*-test; $P = 0.69$).

The settling velocity and equivalent settling diameters after an applied bed shear stress of 0.5 $N\,m^{-2}$ were calculated for those erosion experiments in June and February with a suspended sediment concentration (SSC) higher than 50 $mg\,l^{-1}$. The median settling velocity was 3.4 $mm\,s^{-1}$ and 2.0 $mm\,s^{-1}$ for June and February respectively and the difference was significant (*t*-test, $P = 0.04$). However, the average mean equivalent settling diameter was similar in the two periods (60 µm ± 11 µm in June and 60 µm ± 5 µm in February), which shows that the difference in settling velocities was caused by temperature-induced changes in the viscosity of the seawater, not changes in aggregate size. The mean grain-size of the disaggregated material was about 20 µm. Similar calculations were intended for the experiments in September (dominated by microphytobenthos) but the SSC was too low to allow for a reliable calculation of settling velocities. It was not possible to calculate settling velocities after higher bed shear stresses due to a strong vertical gradient in SSC in the erosion chamber and a grain-size dependent correlation between SSC and OBS-output.

Table 2
Correlation coefficients (r) of the linear regressions between the measured parameters. Numbers in bold: $P < 0.01$.

r	Erosion threshold	Erosion rate[a]	Chl *a*	Org %	Carbohydrates	EPS	Dry dens	Pellet content	Sand content
Erosion rate	**0.64**								
Chl *a*	**0.89**	−0.43							
Org %	0.29	0.00	0.25						
Carbohydrates	**0.91**	−0.42	**0.83**	0.23					
EPS	**0.92**	−0.37	**0.89**	0.35	**0.79**				
Dry dens	0.05	0.19	0.18	**−0.77**	0.00	0.14			
Pellet content	−0.27	−0.00	−0.27	0.25	−0.36	−0.29	0.09		
Sand content	−0.21	0.31	0.13	**−0.69**	0.14	0.19	**0.58**	−0.23	
Cockle density	−0.10	−0.24	0.01	0.01	0.00	0.00	0.17	−0.10	0.00

[a] Log(erosion rate).

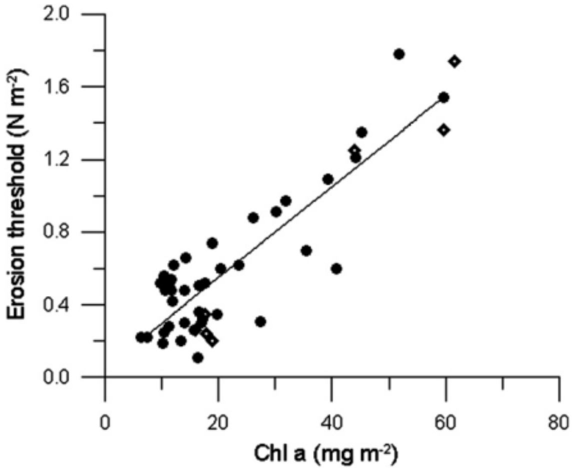

Fig. 4. A plot of the content of chl *a* versus the erosion threshold. Filled circles: EROMES *in situ*; diamonds: EROMES in the laboratory.

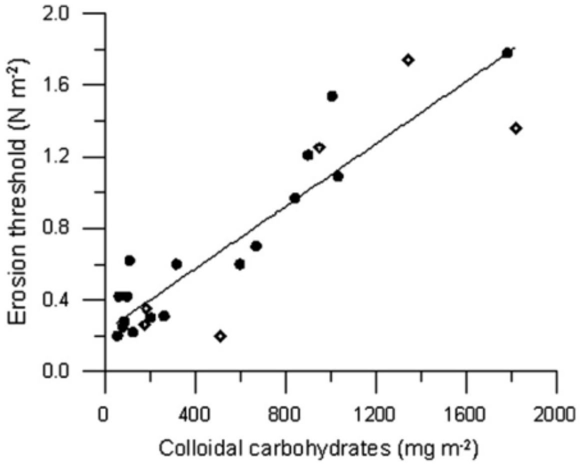

Fig. 5. A plot of the content of colloidal carbohydrates versus the erosion threshold. Filled circles: EROMES *in situ*; diamonds: EROMES in the laboratory.

5. Discussion

5.1. Erodibility, microphytobenthos and macrozoobenthos

The site showed a very visible formation of patchy biofilms created by microphotybenthos (in this environment mainly diatoms) in September 2002 after a long period of relatively sunny and calm weather and again in April 2003. Visible biofilms were not observed during any of the other sampling periods. A pronounced temporal variation in erodibility (erosion threshold and erosion rate) was also observed with generally low erodibility in September and April and higher erodibility during the other sampling periods. A range of erosion thresholds between 0.2 and 1.8 N m^{-2} were observed during the study period and the threshold was strongly correlated to chl *a*, colloidal carbohydrate and EPS. The erodibility was not correlated with any of the other measured physical and biological variables and the data therefore strongly indicates that the variability of erodibility at the site primarily was controlled by microphytobenthos. A similar influence of microphytobenthos has been found in a number of previous studies (e.g. Paterson, 1989; Underwood and Paterson, 1993; Sutherland et al., 1998a; de Brouwer et al., 2000). However, the present correlation between microphytobenthos and erodibility, where the variation in chl *a* content explains about 80% of the variation in erosion thresholds ($r = 0.89$), is stronger than generally observed. Typical correlation coefficients found *in situ* are in the range 0.4–0.6 (Riethmüller et al., 2000; Andersen, 2001; Tolhurst et al., 2006) but the exact dependence between e.g. chl *a* and erosion threshold changes significantly between sites (Riethmüller et al., 2000; Tolhurst et al., 2006). The reason for the strong correlation between chl *a* and erosion threshold found in the present study is the strong correlation which was found between microphytobenthic stock (indirectly quantified by measurements of chl *a*) and the content of colloidal carbohydrates and EPS which have been shown to stabilize cohesive sediments (Paterson, 1989; Yallop et al., 1994; de Brouwer et al., 2002, 2005; Friend et al., 2003; Tolhurst et al., 2006). The secretion of these substances may vary considerably temporally (Sutherland et al., 1998a,b) and therefore, high contents of microphytobenthos will not always be reflected in high contents of colloidal carbohydrates and EPS. However, the data from the present study as well as the study by de Deckere et al. (2002) showed significant correlations *in situ* between chl *a* and both colloidal carbohydrates and EPS. The implication is that at least at some sites chl *a* content will be a good indicator for stabilisation by benthic diatoms. At this particular site simple measurements of chl *a* content will give a good indication of the erodibility. However, the correlation between chl *a* content and sediment erodibility is highly site-specific due to differences in e.g., sediment texture, shelter and biotic community structure and condition as demonstrated by Riethmüller et al. (2000) and Defew et al. (2002). The result of this variability is that in order to be able to predict the sediment erodibility at a specific site, it is generally necessary to carry out site-specific investigations of this relationship. A recent study by Murphy et al. (2008) successfully used multivariate analysis of spectrophotometric measurements to estimate erosion threshold and this may prove to be a useful method in the future.

The markedly higher content of microphytobenthos in September 2002 and April 2003 resulted in a significant increase in the stability of the mudflat at these periods. The content of

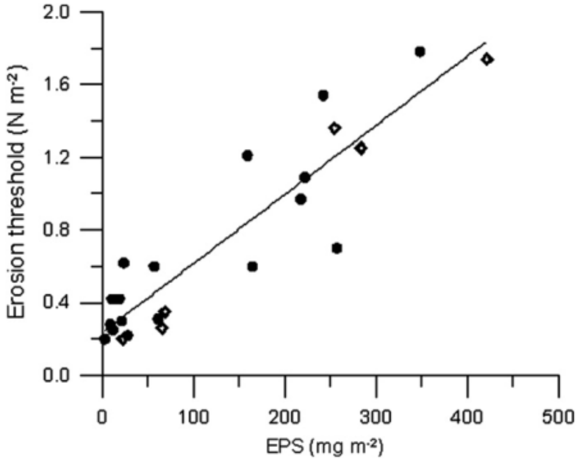

Fig. 6. A plot of the content of EPS versus the erosion threshold. Filled circles: EROMES *in situ*; diamonds: EROMES in the laboratory.

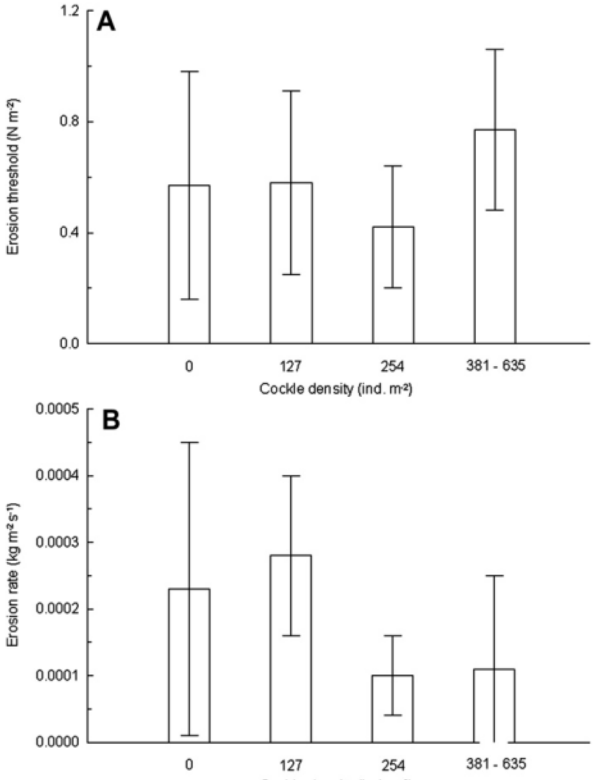

Fig. 7. Erosion threshold (A) and erosion rate (B) as a function of density of cockles in individual erosion cores.

microphytobenthos was low in November 2002 and February 2003 and the bed-level decreased 2 and 3 cm respectively compared to the September level. This general erosion of the site, leaving behind a surface without distinct bedforms, is probably mainly caused by higher wave-activity caused by the generally stronger winds, which prevail at this site in autumn and winter. For example, in August 2002 the average wind speed was 4.8 $m\,s^{-1}$ compared to 7.7 $m\,s^{-1}$ in October when maximum speeds of up to 22 $m\,s^{-1}$ were recorded. However, it is also likely that the lower biomass of microphytobenthos caused by lower light-intensity in autumn and winter will have increased the tendency of erosion of the site. Higher precipitation in the winter may also have reduced the sediment stability (Pilditch et al., 2008; Tolhurst et al., 2008).

The erodibility did not show any correlation with the density of *Cerastoderma edule* which ranged from 0 to 635 ind. m^{-2}. These densities are within the range studied in the laboratory by Ciutat et al. (2006, 2007) who in contrast found a significant increase in erodibility with increasing density of cockles. The effect was argued to be caused by both an increase in bed roughness caused by burrowing activity of the cockles and the exhalent jets from the cockle's siphons. The surface of the mixed mudflat in the present study rarely showed signs of bioturbation induced by the cockles and the cockles were only detectable via small depressions in the sediment surface and the presence of their siphons. The laboratory-result: increase in erodibility due to bioturbation by cockles was therefore not found in the present study *in situ*. The reason for the low level of bioturbation is not known but it may be related to the fact the animals were not disturbed during the experiments as opposed to the laboratory studies by Ciutat et al. (2006, 2007). It is also possible that the very fine-grained texture of the sediment at the site reduces the burrowing activity as indicated by a study by Alexander et al. (1993) who found reduced burrowing rate in fine-grained sediments.

A possible effect of exhalent jets from the cockles was apparently reduced in the present study, maybe due to a difference in turbulence-field and area of foot-print between the EROMES and the annular flume used by Ciutat et al. (2007). With a total bed area of 0.008 m^2 and a distance of only 3 cm between the turbulence-generating propeller and the bed, the EROMES will be less suited for studies of exhalent jets which may protrude at least 10 cm into the water column under low flow conditions (Widdows and Navarro, 2007). These jets will induce an increase in apparent roughness of the bed and this will increase the erosive force of the flow. However, it is not clear from these laboratory experiments if the jets will result in a significant increase in apparent bed roughness under natural intertidal conditions with strong flows induced by both waves and currents.

The biostabilisation indexes, S_b, of 4.7 and 4.3 for September and April respectively are within the range reported for natural sediments *in situ*. Typically values reported are between 3 and 10 (data summarized by Neumeier et al., 2006). The biostabilisation is about 45% stronger than in a laboratory setup with reduced biofilm and a cockle density of 194 ind. m^{-2} reported by Neumeier et al. (2006) who found an index value of 3.1. Their study showed a decrease in S_b when cockles were added to the sediment. The increase in erodibility in the laboratory experiments was partly due to resuspension of bioaggregates from the cockles – bioaggregates that consist of fine-grained material whose probability of settling to the bed is greatly increased because of the filter-feeding activity of the cockles. The bioaggregates are allowed to build up in laboratory experiments but the major part is resuspended by currents and waves in the field (see Section 5.2). The apparent increase in erodibility caused by resuspension of fresh bioaggregates is therefore much smaller in studies carried out *in situ*.

The lack of correlation with contents of Heteromastus pellets could be due to the low variability in pellet contents but the pellets are only suspended at relatively high bed shear stresses, well above the stresses normally required for onset of sediment erosion. This may mask any direct effect of the pellet content as the pellets will only be resuspended in situations where the suspended sediment concentration is already strongly elevated due to the high bed shear stresses.

Also the bivalve *Macoma balthica* and the prosobranch *Hydrobia ulvae* were present at the site but no correlation with erodibility was observed. However, their densities were also much lower than the ones for which Widdows et al. (1998, 2000b), Andersen (2001) and Andersen et al. (2002, 2005) showed significant increases in sediment erodibility.

5.2. *C. edule* and biodeposition

The faeces and pseudo-faeces produced by *Cerastoderma edule* are very fragile and it was not possible to discern any of these after gentle wet-sieving at a 63 μm sieve. This is consistent with the study of Austen (1997) who also found that pellets produced by *C. edule* were rare in sediments from mixed mudflats of the Lister Dyb tidal basin. Due to the fragile nature of the pellets, it was not possible to determine the contribution of these to the total fine-grained content of the surface material. The biodeposition rate of *C. edule* is dependent on the density of the animal, the suspended sediment concentration and perhaps to some extent also season. For a density of 135 ind. m^{-2} in the Oosterschelde, the Netherlands, Smaal et al. (1986) calculated a deposition of 81 g m^{-2} d^{-1}. The density at station A is of the same order (184 ind. m^{-2}) and assuming biodeposition for 300 days each year (allowing for reduced/absent biodeposition during the winter period) a gross-deposition of 24 kg m^{-2} a^{-1} is found. For comparison, with the estimated net-accretion rate of 0.7 cm a^{-1}, the average dry bulk density of 0.98 g cm^{-3} and the average mud content of 35%, the net-deposition of mud at the site is 2.4 kg m^{-2} a^{-1}. This is an order of magnitude lower than the potential gross-deposition induced by the cockles. This indicates that only a small fraction of the bio-deposits is permanently deposited at the site, the majority is resuspended again. A similar conclusion was inferred by Smaal et al. (1986) due to the absence of depletion of suspended sediment in the benthic boundary layer. It also indicates that a substantial part of the fine-grained material deposited at the site could be biodeposits from *C. edule*. This is in accordance with the early observations of Verwey (1952) who found that biodeposits originating from *Mytilus edulis* and *C. edule* made up a significant portion of the total accumulation of fine-grained material in the Dutch Wadden Sea area.

5.3. *Settling velocities of the eroded material*

The analysis of the settling velocities of the eroded material after low bed shear stresses (0.5 N m^{-2}) when sand and fecal pellets from *Heteromastus filiformis* were absent showed that the eroded material had significantly higher equivalent settling diameters than the disaggregated material. This was due to aggregation at the sediment surface, which may be caused both by the presence of microphytobenthos and the biodeposits of *Cerastoderma edule*. It is not possible on the basis of the present data-set to determine which is the most important but given the high biodeposition by *C. edule* calculated above, it is likely that this species contributed substantially to the aggregation. The equivalent settling diameters were in the same range as found for highly aggregated mudflat sediments strongly dominated by fecal pellets by *Hydrobia ulvae* (Andersen and Pejrup, 2002) which shows that the biogenic aggregation of the fine-grained material by *C. edule* and microphytobenthos was substantial. This type of biogenic aggregation has been shown to increase the tendency for net-deposition of fine-grained material (Lumborg et al., 2006) and the increased content of mud will tend to decrease the erodibility of sandy sediment (see Section 5.5). The lack of difference in equivalent settling diameters between June and February was a bit surprising as stronger aggregation in June was expected due to the generally higher biological activity. Such a seasonal variation in aggregation was clearly demonstrated by Andersen and Pejrup (2002) for a mudflat dominated by *H. ulvae*. More samples from different seasons are needed to clarify if the observed lack of temporal difference at the present study site is real but as both *C. edule* and *H. filiformis* are active during the cold season (although with reduced activity), the aggregation may show limited temporal variation.

5.4. *Crest–trough variation*

There was a general tendency towards higher contents of chl *a* and higher erosion thresholds on the crests of the bedforms compared to the troughs but the difference was only significant in part of the study period. There were no significant differences with respect to any of the other measured parameters including dry bulk density, which suggests that the difference in erodibility was also in this case mainly determined by different contents of microphytobenthos (corroborated by the study by Blanchard et al., 2000 and Paterson et al., 2000). However, it is likely that drying will contribute to this difference in erodibility during periods of high evaporation (warm and sunny weather) as demonstrated by Paterson et al. (1990), Widdows et al. (2000b) and Lanuru et al. (2007).

5.5. *Comparison with abiotic erosion thresholds for sand*

The measured erosion thresholds can be compared to the abiotic thresholds for the sand-fraction, which can be computed on the basis of the grain-size. For the grain-size mode of 105 μm a critical bed shear stress of about 0.13 N m^{-2} can be found (Soulsby, 1997). This value cannot be compared directly to the thresholds found *in situ* with the EROMES but the value is considerably lower than the erosion thresholds found *in situ* and the difference cannot solely be ascribed to different erosion criteria. Some of the difference is caused by the presence of fine-grained material (<63 μm), which will increase the threshold. In a study on the erodibility of sand/mud mixtures, Mitchener and Torfs (1996) found that the highest erosion thresholds occurred for sediment mixtures with a mud content of 30–50% depending on mineralogy and grain-sizes. With a mud content of about 35%, the present study site is within this region of maximum erosion thresholds. The estimated erosion threshold of 0.2 N m^{-2} for abiotic conditions is about 50% higher than the threshold calculated for pure sands. This increase is an effect of the mud content and the pelletisation. This threshold-value may also be interpreted as the average erosion threshold for the studied sediments without the effect of benthic diatoms. However, these low thresholds were only observed in about 20% of the erosion experiments and the study confirms that erosion thresholds found in the laboratory on abiotic sediment mostly do not apply in this kind of environment with high biological activity. In contrast to the sand, the cohesive mud-fraction of the sediment will be strongly mediated by the presence of both microphytobenthos and macrozoobenthos. Both surface stabilisation by microphytobenthos and biodeposition and pelletisation by macrozoobenthos will increase the mud content compared to a hypothetical situation without biotic influence. The increased mud content modifies the erodibility of the mixed sediments and is in this way an indirect biotic control on sediment stability. Both *Cerastoderma edule* and *Heteromastus filiformis* are active all-year (although with reduced activity during winter months) and their presence was reflected in the sediment characteristics (fecal pellet content and general aggregation) during every sampling period in the present study.

6. Conclusions

The study demonstrated pronounced temporal variability in sediment erodibility at the studied mixed mudflat. The variability was caused by variability in the presence and strength of biofilms at the sediment surface. The biofilms were formed by microphytobenthos and contents of chl *a*, Colloidal carbohydrates and EPS were inter-correlated and explained about 70% of the variation in erosion threshold.

No effect of density of *Cerastoderma edule* on sediment erodibility was observed. This contrasts with some previous studies carried out in controlled settings in the laboratory. The reason is probably a combination of less burrowing activity of the cockles and more heterogeneous sediment beds in the present study on undisturbed sediments. Any minor direct effect of the cockles may also have been overshadowed by the more effective biostabilizing microphytobenthos. However, an indirect effect on sediment erodibility of the cockles and the polychaete *Heteromastus filiformis* is most likely present as both species will tend to increase the content of fine-grained particles at the sediment surface. This in turn will tend to decrease the erodibility of the sediment surface.

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