

Do benthic diatoms influence erosion thresholds of coastal subtidal sediments?

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Abstract

This study reports diatom cell abundance, concentrations of water-soluble and water-insoluble carbohydrates, and concentrations of chlorophyll—a equivalents as indicators of microbial exudates and biomass in the uppermost sediment layer of two coastal sites (19 m water depth: fine sand; 25 m water depth: mud) in Mecklenburg Bight, south-western Baltic Sea. Correlation analysis with experimentally determined erosion thresholds measured in five different periods of a year showed that the sediment water content and the content of water-soluble carbohydrates may indicate erosion thresholds for both sediment types. Erosion thresholds were significantly negatively correlated with sediment water content at the mud site. At both sites, colloidal carbohydrates, as indicators for diatom EPS, showed significantly negative correlations with sediment water content and no correlation with diatom biomass. Therefore, following current interpretation, we argue that micro-biostabilisation effects of benthic microalgae play a minor role in the investigation area. Light is likely to be insufficient for phototrophic growth on the seafloor of the investigated sites most of the year, as indicated by in situ measurements and calculated values of photosynthetically active radiation. We consider lateral transport of benthic diatoms from shallower to deeper areas of Mecklenburg Bight and subsequent to be the mechanism influencing diatom abundance. Exhaustive biofilms are absent at these depths and mass erosion is not likely to be affected by benthic diatoms.

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1. Introduction

The top layer of coastal sediments constitutes a dynamic system with regard to exchange processes of dissolved and particulate materials. Modelling sediment transport is gaining importance because coastal environments are exposed to increasing stress for instance through dredging and dumping of dredged material. Resuspension curves based solely on sedi-

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mentological parameters do not adequately describe transport processes in natural sediments. Therefore, the influence of biota on sediment erosion becomes a fundamental interest (Krumbein et al., 1994).

Numerous authors who studied erosion on natural sediment surfaces (Grant et al., 1986a, b; De Jonge and Van den Bergen, 1987; Grant and Bathmann, 1987; Grant and Gust, 1987; Riethmueller et al., 2000; Lelieveld et al., 2003) and on artificial ones (Holland et al., 1974; Dade et al., 1990; Paterson, 1990; Meadows et al., 1994) postulate an important role of benthic diatoms in stabilising cohesive and non-cohesive sediments, especially on intertidal mudflats (see Paterson and Black, 1999; Widdows and Brinsley, 2002 for reviews). However, the widely expected relationship between microalgae that produce exopolymeric substances (EPS) mainly consisting of polysaccharide molecules (Decho, 2000) and erosion resistance of sediment surfaces has recently been questioned (Stal, 2003). EPS were found not to be directly involved in stabilisation of sediments but rather to indicate the physiological state of microphytobenthos biofilms (De Brouwer et al., 2003; Orvain et al., 2004). The physiological state and migratory patterns of microalgae have to be considered to explain carbohydrate metabolism and therewith micro-biostabilisation effects (Orvain et al., 2003).

Despite extensive work on intertidal mudflats, little is known about the influence of microalgae on the stability of subtidal sediments. Several papers outline the importance of benthic diatoms for primary production in a wide range of aquatic environments with varying water depths (e.g. Mac Intyre et al., 1996; Cahoon, 1999). There is some evidence in the literature that benthic diatoms, being highly adapted to low light conditions, are capable of growing biofilms and influence sediment stability in areas lacking a regular tidal emersion (Madsen et al., 1993; Sutherland et al., 1998; Lund-Hansen et al., 2002). Benthic diatom mats at a water depth of 30 m were found to contribute significantly to net photosynthesis (Glud et al., 2002).

The aim of this study was to assess the relationship between benthic diatoms and erosion thresholds at two subtidal sites at 19 and 25 m water depth. Erosion thresholds and sediment water content as well as biomass, content of exudates and living conditions

of benthic diatoms in terms of light irradiance were considered on five different sampling dates.

2. Material and methods

2.1. Study sites

The investigation area is situated in Mecklenburg Bight, south-western Baltic Sea (Fig. 1). Tidal currents are negligible and the general current pattern is subject to considerable variations induced by local weather conditions, wind shear and atmospheric pressure variations over the north-east Atlantic, the North Sea and the Baltic (Dickson, 1973). Spatial sediment samples were collected and sedimentological parameters were determined in the investigation area (Bohling, 2003). For erosion experiments, sediment samples were collected at two sites during five cruises: September 2000, April 2001, July 2001, October 2001 and January 2002. The two sites were a fine sand site at 19 m water depth ($54^{\circ} 12.06' \text{ N}$, $11^{\circ} 54.24' \text{ E}$), and a mud site at 25 m water depth ($54^{\circ} 13.26' \text{ N}$, $11^{\circ} 36.96' \text{ E}$).

2.2. Erosion experiments

Sediment cores of 20 cm in diameter were taken with a box corer sampling a sediment area of $\sim 0.1 \text{ m}^2$. Erosion experiments were carried out on board in the erosion device microcosm, into which sediment cores and in situ seawater (overlying water height: 10 cm) were inserted (Ziervogel and Bohling, 2003). The device consists of a removable lid with a stirring disc and a water input and output. Water is pumped into an external water cycle through a central axis and back into the overlying water of the core. By controlling the rotational speed of the disc and the pumping rate, the device generates a spatially homogeneous shear stress velocity (u^*) at the bottom. Calibration of this bottom shear stress in the erosion chamber was done by several approaches, e.g. skin friction probes (Gust and Müller, 1987).

Besides undisturbed sediment cores from each location, cores containing sieved sediment from the upper 5 cm were placed in the microcosm device serving as control cores during erosion experiments. Two thresholds of critical shear stress velocity were

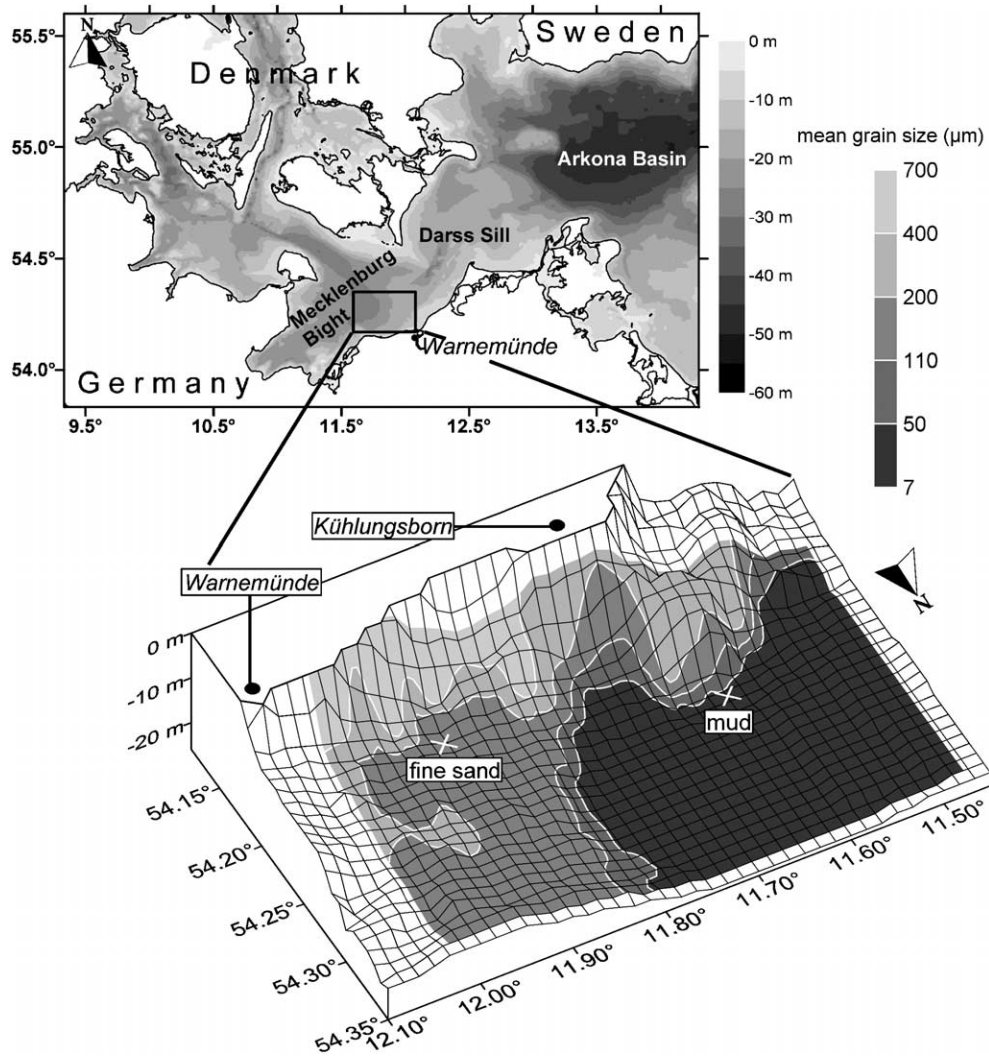


Fig. 1. The study area in Mecklenburg Bight, south-western Baltic Sea (upper part). Grain size distribution of the area with the two sites is shown in the lower part. Bathymetric data derived from (Seifert and Kayser, 1995). An area-wide collection of sediment samples from the upper 5 cm ($n=190$) was conducted by Bohling (2003), who determined sedimentological parameters.

defined describing initial rolling transport of single fine sand grains and loosely bound, fluffy surface material ($u_{cr-initial}^*$) and erosion of the same material ($u_{cr-erosion}^*$). The former threshold was visually specified whereas the latter derived from measurements of total suspended particulate matter (TPM) being entrained into the overlying water of the sediment core. Net erosion fluxes (E), given in Fig. 2, were calculated from differences in TPM at shear stress velocity increments (Tolhurst et al., 2000). The

threshold value ($u_{cr-erosion}^*$) was assessed as the point at which differences in TPM concentrations no longer resulted in negative fluxes (solid line in Fig. 2; $u_{cr-erosion}^* = 0.57 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$). The resulting thresholds were comparable ($\pm 5\%$) to those using a plot of TPM versus u^* (Tolhurst et al., 2000) where the resulting intercept point of two linear regression lines from the plot represents the erosion threshold. Negative values of E may result from methodological accuracy of reweighing filters

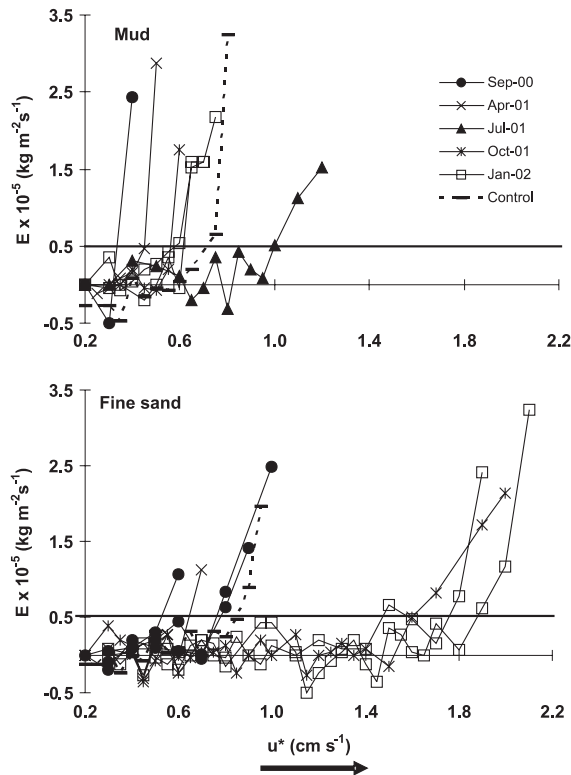


Fig. 2. Erosion flux (E) of fluff from mud (upper graph) and fine sand cores (lower graph) at different sampling dates. Negative values of E may indicate particle deposition during erosion experiments. Dotted lines indicate erosion of control cores with sieved mud and fine sand sediment. Horizontal lines stand for the threshold of $u_{cr-erosion}^*$ ($0.5 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$).

(analytic precision of reweighing filters $\pm 10\%$; Von Bodungen et al., 1991). On the other hand, deposition of particles during the 10 min erosion step may lead to decreasing particle concentration and thus negative calculated values of E , as discussed by Tolhurst et al. (2000).

2.3. Analysis of sediment parameters

After the removal of the 20 cm cores, the remaining sediment surface of the box-corer ($\sim 0.07 \text{ m}^2$) was sampled with plexiglas cores of 36 mm diameter. The upper 5 mm of 3 cores were sliced and frozen at -20°C on board for later analysis representing 3 replicate samples per occasion and site. Water content (% of sediment dry weight) was determined by weighing and drying subsamples to constant weight at 105°C .

Chlorophyll-a (Chl) as an indicator of diatom biomass was measured by the acidification method of Holm-Hansen et al. (1965) using 0.5 cm^3 of defrosted sediment. Chl was extracted in 90% acetone and analysed in a Turner Design Fluorometer (Model 10-AU-005). Calculations of concentrations are based on the JGOFS protocol (UNESCO, 1994). In the presence of chlorophyll-b, chlorophyll-a content may be underestimated seriously using the acidification method (e.g. Daemen, 1986). To test this hypothesis, sandy sediment samples were taken at 1 m water depth at Warnemünde beach (Fig. 1) and Chl concentrations were measured using reserved phase HPLC and the method described above. For Chl determination with HPLC, pigments were extracted in 100% acetone applying ultrasonication and detected by fluorescence emission (excitation: 440 nm, detection: 650 nm). Results of Chl extracted from frozen sediment samples at both -20°C and -80°C by the two different methods were comparable (results not shown). Thus, values of Chl derived from the acidification method provide reasonable results for algal pigment concentrations at the investigated sites.

Colloidal carbohydrate equivalents were extracted from 100 mg of freeze-dried sediment in either 25% saline or 100 mM Na_2EDTA to obtain a water-soluble (Col S) and water-insoluble (Col EDTA) fraction. Carbohydrate concentration as an indicator of diatom EPS was measured using the phenol-sulfuric acid assay (Underwood et al., 1995). The absorbance was measured at 488 nm against a reagent blank. All results are expressed as glucose equivalents per square metre.

One 36 mm core per site was taken in July 2001, October 2001 and January 2002 for enumeration of benthic diatom cells. Sediment from the upper 5 mm of each core was sliced and preserved with formaldehyde at a final concentration of 4%. Diatom cells were counted after 2 min ultrasonication using an inverted microscope according to Utermöhl (1958).

2.4. Irradiance measurements

A 12 h time series of photosynthetic active radiation (PAR, equal quantum response from 400 to 700 nm) was recorded at the mud station in July 2001 using a calibrated Log Quantum Scalar Irradiance Sensor (QSP-200L; Biospheric Instruments Inc., San

Diego) mounted on top of a CTD frame (Turnewitsch and Graf, 2003). The sensor had a spin-off value of $0.85 \mu\text{E m}^{-2} \text{s}^{-1}$. Information on total daily surface irradiance and wind speed during the cruises in July 2001, October 2001 and January 2002 was obtained from shipboard meteorological measurements. Sub-surface irradiance (I_0) was calculated from surface irradiance measurements and reflection of irradiance at the sea surface depending on wind speed and solar irradiation using the scheme provided by Walsby (1997). Depth-depending PAR was assessed using the exponential light extinction equation:

$$I_z = I_0 e^{-kz} \quad (1)$$

where I_z ($\mu\text{E m}^{-2} \text{s}^{-1}$) is the irradiance at a water depth z (m). Two different attenuation coefficients (k) were used to determine bottom values of PAR. We used the highest and the lowest k -values (0.2 and 0.5) measured during the 12 h series in July 2001. The latter corresponds to the mean k value for coastal Baltic waters given by Dera (1995).

2.5. Statistical analysis

All measured data from biochemical sediment analysis were assumed to be normally distributed. This was tested by taking 13 samples of 36 mm plexiglas cores from one box-corer at the fine sand site in September 2000. Chl was measured in the upper 5 mm of each core by the acidification method as described above. Values of Chl were normally distributed about the mean ($P < 0.05$; results not shown).

Pearson's correlation coefficients (r) were calculated to examine relationships between mean con-

centrations of sediment parameters and erosion thresholds. Mean $u_{\text{cr-erosion}}^*$ values were used for calculations of r when, for erosion experiments, duplicate fine sand cores were taken in September 2000 and January 2002, and mud cores in January 2002. The values of significance were calculated using a t-test. Differences between values of sediment parameters were examined using an analysis of variance (one-way ANOVA) at a 5% significance level.

3. Results

3.1. Erosion behaviour of mud cores

Sediment surfaces at the mud site were covered by a homogenous fluffy layer at each sampling occasion. The thickness of fluff varied between a few mm in January 2002 and about 1 cm in September 2000. Differences in erosion behaviour of duplicate cores were tested in January 2002 and found to be negligible (Fig. 2). Values for $u_{\text{cr-erosion}}^*$ varied between 0.4 cm s^{-1} in September 2000 and 0.625 cm s^{-1} in January 2002 (mean value of $n=2$), except for July 2001. Here, $u_{\text{cr-erosion}}^*$ increased up to 1.0 cm s^{-1} exceeding the threshold value of 0.75 cm s^{-1} for sieved mud (dotted line in the upper graph of Fig. 2). Generally, thresholds of $u_{\text{cr-erosion}}^*$ varied by a factor of 2 at this location. The threshold of initial particle transport showed a variation by a factor of 1.6 during the sampling period, with the highest value in July 2001 (0.5 cm s^{-1}). A significant positive relationship was found between both thresholds ($r=0.89$, $P < 0.1$, $n=5$, Table 1).

Table 1

Pearsons' correlation coefficients between erosion thresholds and mean values of different parameters in the top 5 mm from the fine sand and mud stations ($n=5$; $n=4$)

	Mud (25 m)					Fine sand (19 m)				
	$u_{\text{cr-initial}}^*$	$u_{\text{cr-erosion}}^*$	Col S	Col EDTA	Chl	$u_{\text{cr-initial}}^*$	$u_{\text{cr-erosion}}^*$	Col S	Col EDTA	Chl
$u_{\text{cr-erosion}}^*$	0.89*					0.97*** ^a				
Col S	0.99***	0.91**				0.14	0.71 ^a			
Col EDTA	0.63	0.33	0.66			0.41	-0.01 ^a	-0.52		
Chl	0.57	0.19	0.53	0.78		-0.17	-0.01 ^a	0.09	0.27	
Water content	-0.95**	-0.90**	-0.97***	-0.66	-0.58	0.15	0.54 ^a	-0.84*	0.50	-0.55

$u_{\text{cr-initial}}^*$ - critical shear stress velocity for initial rolling transport, $u_{\text{cr-erosion}}^*$ - critical shear stress velocity for particle erosion, Col S - carbohydrate fraction extracted with saline, Col EDTA - carbohydrate fraction extracted with EDTA, Chl - Chlorophyll-a equivalents. Values of r are significant at: ***= $P < 0.01$, **= $P < 0.05$, *= $P < 0.1$.

3.2. Erosion behaviour of fine sand cores

At the fine sand site, sediment surfaces were more heterogeneous compared to the mud cores because of sediment ripples and biogenic structures (mussel shells and worm tubes). Fluff was also present between ripples but to a lower extent than at the mud site. Still, variations in erosion behaviour remained low among replicate cores in September 2000 and January 2002 (lower graph of Fig. 2). The lowest value for $u_{cr-erosion}^*$ was 0.7 cm s^{-1} measured in September 2000 (mean value of $n=3$) and April 2001. In October 2001 and January 2002 (mean value of $n=2$) the highest value of $u_{cr-erosion}^*$ of 1.7 cm s^{-1} was measured, exceeding the threshold value of 0.9 cm s^{-1} for sieved fine sand sediment (dotted line in the lower graph of Fig. 2). Thus, during the sampling period, $u_{cr-erosion}^*$ varied by a factor of 2.4 at this location.

In September 2000 and April 2001, initial particle transport was detected at 0.4 and 0.35 cm s^{-1} , respectively. Values for $u_{cr-initial}^*$ increased to 0.55 and 0.6 cm s^{-1} in October 2001 and January 2002, respectively, compared to former sampling dates (factor 1.7). As calculated for the mud cores, a positive significant correlation was found between $u_{cr-initial}^*$ and $u_{cr-erosion}^*$ ($r=0.97$, $P<0.05$, $n=4$, Table 1).

3.3. Carbohydrate concentrations

At the mud site, mean concentrations of water-soluble carbohydrates (Col S) were significantly different from one another ($F_{3,48}=28.32$, $P<0.001$). The highest single Col S value of $3.4 \text{ g glucose equiv. m}^{-2}$ (mean: 2.8) was measured in July 2001 whereas the lowest value of $0.4 \text{ g glucose equiv. m}^{-2}$ was measured in September 2000 (Table 2). Here, no significant differences were found comparing mean values of water-insoluble carbohydrates (Col EDTA) ranging between 0.8 and $1.5 \text{ g glucose equiv. m}^{-2}$ ($F_{3,48}=1.12$, $P=0.4$). At the fine sand site, mean values of Col S exceeded those from the mud site, except for July 2001. Col S were significantly different from one another ($F_{3,48}=17.57$, $P<0.001$) and from values at the mud site ($F_{2,4}=22.73$, $P<0.001$) ranging between $0.2 \text{ g glucose equiv. m}^{-2}$ in July 2001 and $10.5 \text{ g glucose equiv. m}^{-2}$ in January 2002. Concentrations of Col EDTA were significantly dif-

Table 2
Mean values (\pm SD) of carbohydrate fractions (Col S, Col EDTA) and chlorophyll-a (Chl), median diatom cell abundances in the top 5 mm ($n=3$), and erosion threshold values († mean values of $n=2$; ‡ mean value of $n=3$) from the fine sand and mud station at different sampling dates

	Mud (2.5 m)					Fine sand (19 m)				
	Sep 00	Apr 01	Jul 01	Oct 01	Jan 02	Sep 00	Apr 01	Jul 01	Oct 01	Jan 02
Col S (g m^{-2})	0.46 ± 0.06	1.41 ± 0.28	2.81 ± 0.55	1.36 ± 0.05	0.85 ± 0.17	1.83 ± 0.42	5.46 ± 0.53	0.22 ± 0.07	5.17 ± 3.17	9.57 ± 0.84
Col EDTA (g m^{-2})	1.19 ± 0.37	1.34 ± 0.05	1.36 ± 0.13	1.17 ± 0.17	1 ± 0.31	0.08 ± 0.05	0.15 ± 0.07	0.28 ± 0.09	0.12 ± 0.07	0.11 ± 0.04
Chl (g m^{-2})	0.9 ± 0.15	7.04 ± 0.34	4.2 ± 0.11	2.34 ± 0.28	1.17 ± 0.17	4.45 ± 0.43	26.08 ± 1.18	15.5 ± 0.44	22.99 ± 1.73	9.14 ± 0.42
Pennate diatoms (10^5 cm^{-2})	n.d.	n.d.	5	6	34	n.d.	n.d.	8	7	26
$u_{cr-initial}^*$ (cm s^{-1})	0.3	0.4	0.5	0.4	0.35	0.4	0.35	n.d.	0.55	0.6
$u_{cr-erosion}^*$ (cm s^{-1})	0.4	0.5	1	0.6	0.625^{\ddagger}	0.73^{\ddagger}	0.7	n.d.	1.6	1.7^{\ddagger}

n.d.=not determined.

ferent from one another ($F_{3,48}=4.21$, $P=0.03$) and from values at the mud site ($F_{2,4}=32.5$, $P<0.001$) varying between 0.01 and 0.4 g glucose equiv. m^{-2} . Highest values were measured in July 2001.

3.4. Chlorophyll-*a* equivalents

Concentrations of Chl at the mud site ranged between 0.7 $mg\ m^{-2}$ in September 2000 and 7.3 $mg\ m^{-2}$ in April 2001 (Table 2), being significantly different from one another ($F_{3,48}=383.3$, $P<0.001$). At the fine sand site, concentrations of Chl were higher than at the mud site, varying significantly from one another ($F_{3,48}=250.6$, $P<0.001$). Values ranged between 4.2 $mg\ m^{-2}$ in September 2000 and 27 $mg\ m^{-2}$ in April 2001.

3.5. Diatom abundances

Cell numbers at both stations varied between 5 and $8 \times 10^5\ m^{-2}$ in July and October 2001 with slightly higher values at the fine sand site (Table 2). In January 2002 this pattern reversed, with diatom abundances increasing to $26 \times 10^5\ cm^{-2}$ at the fine sand site and $34 \times 10^5\ cm^{-2}$ at the mud site.

3.6. Sediment parameters and erosion thresholds

At the mud station, Col S was significantly positive correlated with both erosion thresholds (Table 1). The sediment water content showed significantly negative correlations with both erosion thresholds at the mud site and Col S at the mud and the fine sand site. Mean values of Chl and Col EDTA did not correlate significantly with any of the remaining parameters, although parameters showed a positive but not significant relationship with each other and $u_{cr-initial}^*$.

At the fine sand site, mean concentration of Col S and sediment water content were found to be significantly negative correlated. Erosion thresholds were not significantly correlated with any of the analysed parameters, although Col S and $u_{cr-erosion}^*$ showed a positive but not significant relationship.

3.7. Irradiance at the mud site

Weather conditions in the investigation area in July 2001 were calm and sunny (high pressure, 1015 hPa)

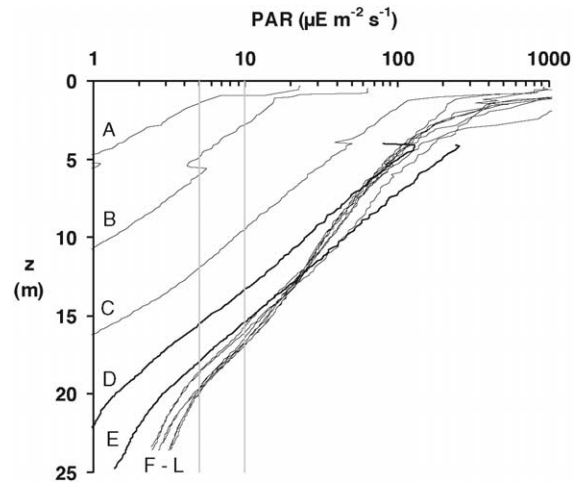


Fig. 3. Vertical profiles of photosynthetic active radiation (PAR) in the water column of the mud station in July 2001. a - 2:45 h, b - 3:00 h, c - 4:00 h, d - 5:00 h, e - 6:00 h, f - 9:30 h, g - 10:00 h, h - 10:30 h, i - 11:30 h, j - 12:00, k - 12:30 h, l - 13:00 h (h in UTC). The vertical box indicates lower limit of light intensities for benthic microalgae growth ($5 - 10\ \mu E\ m^{-2}\ s^{-1}$) as given by Cahoon (1999).

and illumination is therefore considered to be optimal. Results of light intensity measurements showed an exponential decrease from surface waters to the bottom. On the seafloor, PAR reached highest values around midday (Fig. 3). During the entire measurement period, PAR did not reach $5\ \mu E\ m^{-2}\ s^{-1}$ at water depths exceeding 20 m. Fitting Eq. (1) to the in situ PAR data, attenuation coefficient (k) varied between 0.2 and 0.5.

4. Discussion

The significantly negative correlation between sediment water content and erosion thresholds at the mud site indicates the importance of a fluffy layer in terms of sediment transport processes. The unconsolidated surface layer, with water contents of 85–98% of dry weight, was resuspended under low hydrodynamic conditions. Water-soluble carbohydrates (Col S) remained the only parameter showing significantly positive correlations with erosion thresholds. This finding agrees with results of numerous authors calculating significantly positive relationships between erosion thresholds and colloidal carbohydrates, and

thus, predicting micro-biostabilisation effects on intertidal sediment surfaces (Underwood and Paterson, 1993; Christie et al., 2000; Yallop et al., 2000). Sutherland et al. (1998), who worked in a subtidal area, also found strong relationships between erosion thresholds, determined in situ, and sediment chlorophyll and colloidal carbohydrate content.

In our study, stronger relationships between sediment parameters and erosion thresholds were found at the mud station than at the fine sand station. This was probably caused by lower $u_{cr-erosion}^*$ values at the fine sand than at the mud site. However, relationships of sediment attributes may also be influenced by differences in sediment surface topography of the sampled cores as described above. The homogenous topography at the mud site resulted in low variations of sediment parameters and erosion thresholds. The surfaces of the fine sand cores were to a varying extent covered by biotic and abiotic structures such as ripples. This topography may have led to a patchier distribution of sediment properties and microphyto-benthic biomass in the sampling area of the box-corer compared to the mud site. Sundbaeck (1984) and Glud et al. (2002) found variations of diatom biomass on a spatial scale of metres. Grant et al. (1986a) described patchy distribution of Chl on a centimetre scale. In the latter study, selective rolling transport and entrainment of exposed sand particles attached to algae on ripple crests induced a patchy distribution of photopigments. Such processes may also explain the patchy distribution of sediment parameters at our fine sand station.

A lack of correlation between Chl and both Col S and Col EDTA indicates discrepancies between these parameters. Other studies illustrate that the relationship between diatom biomass and exudates is not simple. While a significant correlation between Col EDTA and Chl was reported by e.g. Van Duyl et al. (2000), only the loosely bound fraction of carbohydrates (Col S) correlated with diatom biomass in the studies of De Brouwer et al. (2000, 2003). Supporting the present results, no relationship between exudates and Chl was found by Madsen et al. (1993). There are some suggestions in the literature that short-term dynamics of Chl and EPS within benthic diatom assemblages may not be coupled and depend on the physiological state of the diatoms (e.g. Orvain et al., 2003). Moreover, exudates produced by micro-

organisms have a short half-life, being rapidly dissolved into the overlying water (Blanchard et al., 2000). The significantly negative correlation between Col S and the sediment water content found here at both sites may reflect this process. The content of algal biomass on sediment surfaces may also be affected by benthic grazers and bioturbators. The mud snail *Hydrobia ulvae* is known to feed on benthic diatoms, thus decreasing erosion thresholds of sandy sediments (Andersen, 2001). On the other hand, benthic meio- and macro-organisms may generate exudates as suggested by Meadows and Tait (1989) and Mouritsen et al. (1998). Finally, bacteria also contribute to the EPS pool (Decho and Moriarty, 1990).

Benthic diatoms were more abundant at the fine sand station than at the mud station in July and October 2001. Cell numbers found here correspond to diatom abundances determined in Laholm Bay, south-eastern Kattegat, monitored over a one-year period at water depths of 0–30 m (Sundbaeck, 1986; Sundbaeck and Joensson, 1988). Sundbaeck (1986) found highest rates of benthic primary production at 14–16 m water depth with light intensities of $20 \mu\text{E m}^{-2} \text{s}^{-1}$. Average values of PAR still permitting phototrophic growth are given as 5–10 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Cahoon, 1999). In an Arctic fjord, Glud et al. (2002) demonstrated that benthic diatoms adapt their photosynthetic apparatus to changing light conditions. The authors measured net photosynthesis in a diatom mat down to $4.5 \mu\text{E m}^{-2} \text{s}^{-1}$, confirming the values of Cahoon (1999). However, studies dealing with micro-biostabilisation effects of sediment surfaces reported increased diatom biomass and concurrently increased erosion thresholds under higher PAR values (e.g. 600–1700 $\mu\text{E m}^{-2} \text{s}^{-1}$, Paterson et al., 1990). In these light-saturated environments both photosynthesis and production of exudates were found to be strictly connected (Smith and Underwood, 1998; De Winder et al., 1999; Staats et al., 2000). Sutherland et al. (1998) determined micro-biostabilisation effects at an average water depth of 1–2 m, whereas Madsen et al. (1993) demonstrated that benthic diatom growth increased erosion thresholds with time in shallow water sediments when incubated at $200 \mu\text{E m}^{-2} \text{s}^{-1}$ in the laboratory. In Mecklenburg Bight such light intensities are typically reached at 0–5 m water depth, a depth interval com-

prising 10% of the area of Mecklenburg Bight (Seifert and Kayser, 1995). On the other hand, light intensities predominant on the seafloor of the fine sand site and the mud site were of the order of, and even less than, average values given by Cahoon (1999). Environmental conditions supporting photosynthesis and EPS production were best in July 2001 and became suboptimal in October 2001 and January 2002 (Fig. 4). In contrast to suboptimal light conditions, diatom cell abundances as well as $u_{\text{cr-erosion}}^*$ and Col S were highest in January 2002. These findings may be an indicator of micro-biostabilisation effects; however, values of $u_{\text{cr-erosion}}^*$ and Col S were found to

be lowest in July 2001, in disagreement with light conditions.

What mechanism can have caused the observed patterns of diatom abundances? Considering the results of the PAR measurements, increasing diatom cell numbers can hardly be explained by an on-site growth at water depths of approximately 20 m in the investigation area. It is more likely that resuspension followed by lateral transport finally depositing the algae in the basin of Mecklenburg Bight induces spatial distribution of benthic diatoms, as proposed by e.g. Sundbaeck and Joensson (1988). Microscopical examination of experimentally resuspended fluff from the mud site revealed pennate diatom cells incorporated into fluffy layer material, supporting this hypothesis. This mechanism would explain higher cell abundances at the mud station than at the fine sand site in January 2002.

5. Conclusion

The influence of microphytobenthos on sediment stability at water depths exceeding 20 m can virtually be excluded in the investigation area. The stability of the sediment at the mud site is primarily a function of water content and Col S (Table 1). The source of Col S remains unknown, although the PAR levels indicate that it is not from actively photosynthesing organisms. At the fine sand site, micro-biostabilisation is less significant, although the data indicate that Col S may affect $u_{\text{cr-erosion}}^*$ (Table 1). Diatoms are known to be capable of heterotrophic growth (Admiraal and Peletier, 1979) and EPS production in the dark (Underwood and Smith, 1998). However, results of modelled and in situ measured PAR indicate that net photosynthesis and production of exudates are restricted to calm weather with optimal light conditions. In shallower parts of Mecklenburg Bight, e.g. at less than 5 m depth, PAR may reach values allowing micro-biostabilisation of sediment surfaces. Although little is known about microphytobenthos abundance in these shallow parts, phototrophic growth and micro-biostabilisation of sediment surfaces are likely to be limited to these areas, which encompass approximately 10% of the total area of Mecklenburg Bight. Thus, 90% of the area remains little affected by micro-biostabilisation of phototrophic diatoms.

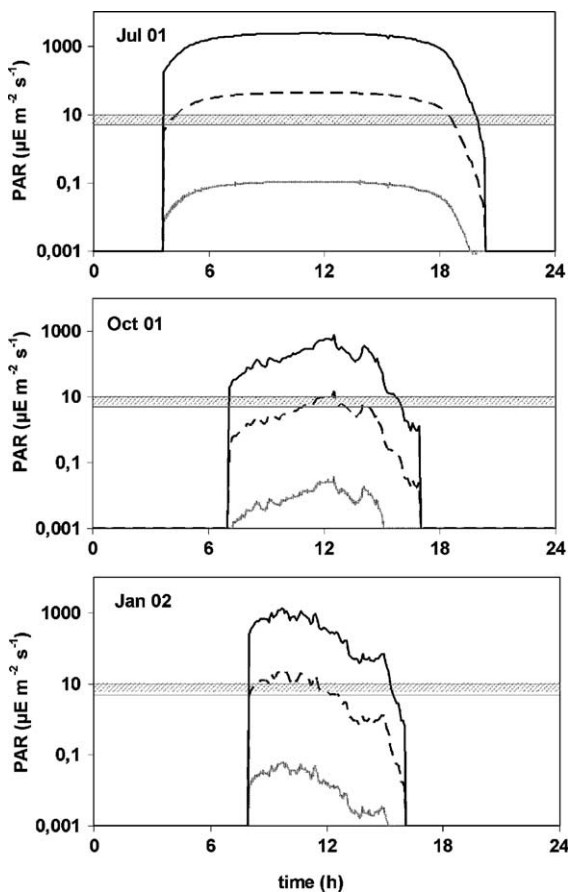


Fig. 4. Subsurface light intensities (solid lines) calculated from surface PAR measured on board and calculated PAR at the bottom (20 m water depth) using an attenuation coefficient of 0.2 (dashed lines) and 0.5 (dotted lines). Horizontal boxes indicate lower limit of PAR permitting phototrophic growth ($5 - 10 \mu\text{E m}^{-2} \text{s}^{-1}$) as given by Cahoon (1999).

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