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# A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics

NORA NOFFKE*[1] and WOLFGANG E. KRUMBEIN†
*Carl von Ossietzky University Oldenburg, Marine Laboratory of the Institute for Chemistry and Biology of the Marine Environment (ICBM), Schleusenstr. 1, 26382 Wilhelmshaven, Germany*
*†Carl von Ossietzky University Oldenburg, Institute for Chemistry and Biology of the Marine Environment (ICBM), PO Box 2503, 26111 Oldenburg, Germany*
*[1]Present address: Universität Frankfurt/Main, Geologisch-Paläontologisches Institut, Senckenberganlage 32–34, 60054 Frankfurt/Main, Germany*

## ABSTRACT

In the tidal flats of Mellum Island (southern North Sea), biofilms and microbial mats, generated largely by cyanobacteria, colonize the sedimentary surfaces. Biostabilization effects and biomass enrichment influence erosional and depositional dynamics resulting from tidal flushing and storm surges. The overlapping of both biological and physical forces causes the development of characteristic sedimentary structures. To obtain a quantitative expression of the degree of effectiveness of microbial colonization in the formation of structures in an extended tidal area, a modification index (MOD-I) was developed based on the following values: (i) the proportion of mat-covered area related to a defined investigation area ($I_A$); (ii) the degree of steepness of slope angles of raised erosional remnants ($I_S$); and (iii) the degree of microbial levelling of a rippled sedimentary surface ($I_N$). The MOD-I was calculated for several defined regions within the study area, and both winter and summer situations were considered. The MOD-I values show, first, that the lower intertidal zone is characterized by index values approaching zero. This implies that microbially induced effects in this zone are negligible, even in summer. Second, the upper intertidal zone is characterized by lower index values in winter and relatively high values in summer. This implies a predominantly seasonal control on the biofilm development in this zone. Third, in the lower supratidal zone, the index values are almost identical during both winter and summer. This implies non-seasonal biological effects in this zone. Concomitant empirical studies on the composition of microbial mats and films suggest that the dominant microbial type influences the MOD-I value.

**Keywords** Benthic cyanobacteria, microbially induced sedimentary structures, quantification of microbial influence, Recent, siliciclastic tidal flats.

## INTRODUCTION

Biofilms are aggregates of microbial cells and their extracellular polymeric substances (EPS) (Charaklis & Marshall, 1989). They develop on all kinds of interfaces by adsorption (Neu, 1994) and can cover substrate surfaces completely. Sediments of aquatic systems provide excellent substrata for biofilm development (Decho, 1990), and thick organic layers develop locally on sedimentary surfaces. These are termed microbial mats (Krumbein, 1983). According to Neu (1994), microbial mats can be regarded as advanced stages of biofilm development. In many tidal flats, benthic phototrophic microbes are involved in biofilm production, and cyanobacteria play a major role. These microorganisms are most abundant in the upper intertidal and lower supratidal zones (Gerdes & Krumbein, 1987).

The activities of cyanobacteria may influence the erosional and depositional dynamics of sediment systems. The interplay between both biological and physical forces results in the formation of characteristic sedimentary structures. Coherent biofilm matrices, consisting of cyanobacteria and their EPS, fix and glue together the surface sediments (De Boer, 1981; Paterson & Daborn, 1991). Microbial fixation of sediment is known as biostabilization, and it increases stability against erosion. Overlapping of biostabilization and erosion causes a characteristic surface relief, named erosional remnants and pockets (Reineck, 1979; Wunderlich, 1979; Gerdes *et al.*, 1993). Erosional remnants are relict, table-like, raised areas of the sediment surface, which are covered by a microbial mat layer. The remnants alternate with erosional pockets, deeper lying, rippled surface parts not visibly colonized by microorganisms. The structure evolves by local destruction of the tissue-like organic layer formerly covering the whole tidal surface and sheltering the underlying sediment against erosion.

Biomass enrichment as well as trapping and binding of mineral particles by the microbes give rise to a phenomenon termed Oberflächen-Nivellierung – surface levelling (Noffke *et al.*, 1996; Noffke, 1997). Differences in the sedimentary surface relief induce distinct ecological responses by bacteria: deeper parts of the surface morphology, e.g. ripple mark valleys, are localities of higher biomass production, as ecological conditions (e.g. humidity) at these protected sites are more favourable compared with more exposed sites. The biomass below the uppermost, living mat layer consists of EPS as well as degraded sheaths and trichomes of former cyanobacterial generations. Mineral grains can also be found, which were incorporated into the organic matrix by former trapping and binding processes. These processes influence the depositional dynamics prevailing in tidal environments (Gerdes *et al.*, 1993, Noffke *et al.*, 1997). Owing to these bacterial activities, the original, physically modelled morphology of sedimentary surfaces becomes levelled in the course of time, and the final morphological stage is a planar surface.

While biostabilization and organic/mineral accumulation are known processes in structure formation, a quantitative expression of such structural changes in an extended tidal area is still lacking. In this study, the aim was to develop an index of the degree of spatial and/or seasonal microbial influence on the formation of sedimentary structures in tidal flats. The index was to be based on the following parameters obtained from the surface relief: (i) area of the mat-covered sedimentary surface proportional to a defined investigation area; (ii) degree of steepness of slope angles of the raised erosional remnants; and (iii) the degree of microbially induced levelling of the rippled sedimentary surface. In this paper, we present a calculation method and its application to a tidal flat relief.

## STUDY AREA

Mellum Island is located in the southern North Sea (Fig. 1a). The sediments consist mainly of well-sorted (0·100–0·200 mm) quartz sands. The climatic conditions of the area are characterized by a mean annual temperature of 17°C, frequent precipitation and prevailing westerly winds. Winter storms are frequent, and the mean tidal range is about 2·9 m.

Biofilms and microbial mats on Mellum Island have been studied in detail (Gerdes *et al.*, 1985; Stal & Krumbein, 1985; Villbrandt, 1992; Noffke, 1997). Two morphotypes of cyanobacteria are typically involved: (i) filamentous forms (dominant species being *Microcoleus chthonoplastes* and *Oscillatoria limosa*) that tend to interweave the sedimentary particles and to produce cohesive, tissue-like organic layers; and (ii) coccoid unicells (e.g. *Merismopedia punctata*). The latter do not form true mats but are dispersed in the upper translucent layers of the sediments, glueing together the mineral grains by their EPS.

## METHODS

### Field investigations and calculations

On the tidal flats, quadrats for investigation were established along two transects (Fig. 1b). Transect 1 led from mean low water (MLW) to mean high water (MHW) and was directed to the NNE. Transect 2 was more or less perpendicular to transect 1 and directed from SE to NW.

As erosional remnants and pockets can reach several m$^2$ in area, a size of 10 m × 10 m was chosen for the quadrats. To calculate the degree of microbial impact on the depositional system, the following geometric data were collected randomly in each quadrat (Fig. 2a–c). Based on the field data, three subindices were developed. The aim

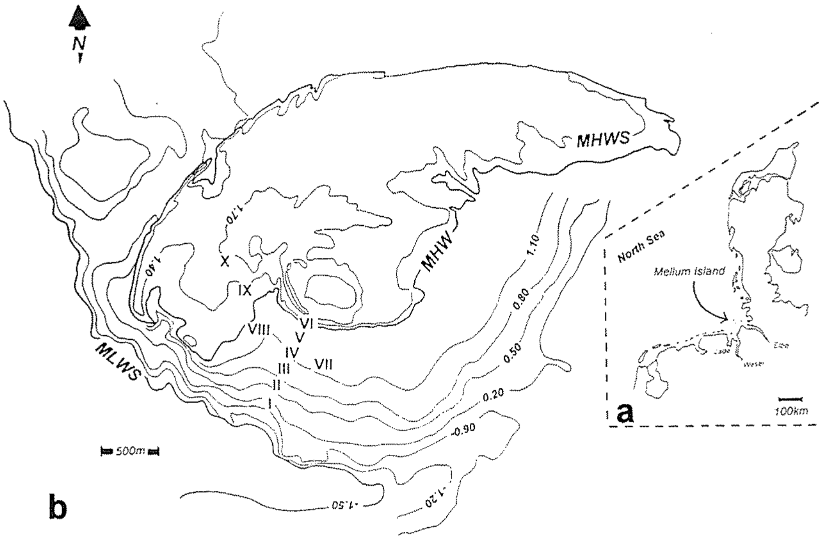

**Fig. 1.** Study area. (a) Location of Mellum Island in the southern North Sea. (b) Location of transects and investigated stations across the back-barrier tidal flats. Transect 1 from about SSW to NNE, investigated stations I–VI; transect 2 from about SE to NW, investigated stations VII–X.

was to gain subindex values ranging between zero (no measurable microbial influence) and 1 (maximum biological impact).

### *The proportion of sedimentary surface covered by microbial mats ($A_m$) related to the total quadrat area ($A_i$)*

For example, Fig. 3a shows a slightly elevated erosional remnant stabilized by a thin microbial mat layer. Seen from above, mat-covered areas ($A_m$) have an irregular shape. To determine their extent, these surface parts were divided into rectangles ($A_1 \ldots A_n$; Fig. 2a). The sum of all rectangle contents approaches the actual dimension of the mat-covered area, expressed in m$^2$:

$$A_1 + A_2 + A_3 + \ldots + A_n \approx A_m.$$

From this, an index ratio ($I_A$) was deduced to describe the proportion of mat-covered areas ($A_m$) related to the whole investigation square ($A_i$):

$$I_A = \frac{A_m}{A_i}. \tag{1}$$

### *Slope angles of the raised erosional remnants*

The steepness of slope angles of the raised erosional remnants (e.g. Fig. 3b) was determined by measuring the angles ($\alpha$) in transverse sections across margins of the erosional remnants (Fig. 2b); two to four measurements were taken per remnant ($A_1 \ldots A_n$, see above). The values are expressed in degrees. In order to calculate a dimensionless index number ($I_s$), the sine values of the measured angles were used:

$$I_s = \sin \alpha \tag{2}$$

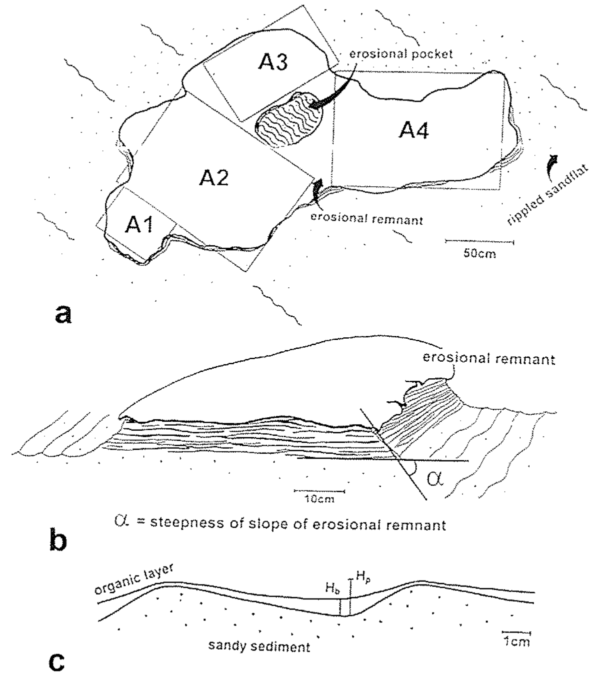

**Fig. 2.** Measured variables. (a) Determination of area of irregularly shaped microbial mat-covered area (plan view). (b) Determination of the steepness of the slope of an elevated erosional remnant in a transverse section. (c) Determination of the degree of microbial surface levelling in a transverse section through mat-covered ripple marks. $H_b$, thickness of microbial mat layer; $H_p$, height of physical ripple mark.

### *The degree of microbial levelling of ripple marks*

For example, Fig. 3c shows a transverse section through ripple marks covered by a thick organic layer. The degree of surface levelling ($I_N$) was deduced from the heights of non-colonized ripple marks ($H_p$ = the straight line from the trough point to the summit point of the ripple mark) minus the thickness of the microbial cover ($H_b$) in the ripple valleys. One measurement expressed in centimetres was taken per rectangle ($A_1 \ldots A_n$, see above) in transverse sections of the rippled sediment (Fig. 2c). The index of surface levelling is therefore defined by

$$I_N = 1 - \left[\frac{(H_p - H_b}{H_p)}\right] \qquad [H_p > H_b > 0] \qquad (3)$$

According to the different microbial influences (surface stabilization, accumulation of biomass and mineral grains), all three subindices (Eqs 1–3) have to be considered in evaluating the general microbial influence on the formation of sedimentary structures for each locality on tidal flats:

$$\left[\frac{A_m}{A_i}\right] \times \sin\alpha \times 1 - \left[\frac{(H_p - H_b}{H_p)}\right] = \text{MOD-I}\ [H_p > 0] \qquad (4)$$

'MOD-I' is the modification index that expresses microbial vs. physical effects on the surface relief. To produce modification indices ranging between zero and one, which correspond with the subindices, the three parts of the equation are multiplied. Modification indices approaching zero describe low microbial influence; modification indices near 1 represent high microbial influence.

## Concomitant empirical studies on the microbial communities

Ten samples of benthic microorganisms were taken from the sedimentary surfaces of each investigation square, and fixed in 4% formaldehyde diluted in filtered sea water. Microbes were examined by light microscopy. The relative abundance of the major mat and biofilm producers (*Microcoleus chthonoplastes*, *Oscillatoria limosa*, *Merismopedia punctata*) was estimated according the method described by Riege (1994). To determine the frequency of the different species, four categories were defined:

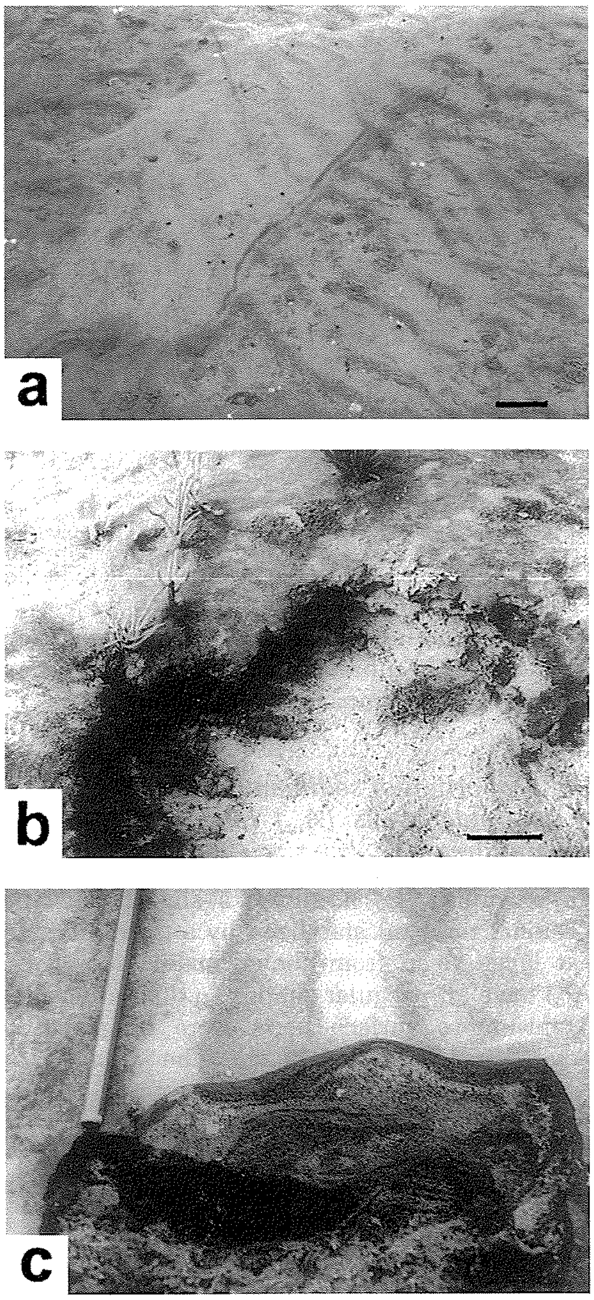

**Fig. 3.** (a) Microbial mat-stabilized erosional remnant of the sedimentary surface of the intertidal zone, Mellum Island. $I_A$ describes the proportion of sedimentary surface covered by mats relative to the sample quadrat area. (b) Steep slope of a raised mat-covered erosional remnant, lower supratidal zone, Mellum Island. $I_S$ quantifies the angle of slope. (c) Vertical section through a mat-covered tidal sediment, lower supratidal zone, Mellum Island. Valleys of ripple marks of a former sedimentary surface are filled by organic material. $I_N$ defines the degree of microbial levelling of the sedimentary surface.

rare – one or two specimens per slide;
common – several specimens per slide;

frequent – several specimens in each section of the slide;

dominant – specimens frequent in each section of the slide.

Field work was carried out in February and September 1995 to obtain comparative data from winter and summer situations: in February, biomass productivity was low; in September, cyanobacterial development reaches its annual maximum (Wachendörfer, 1991).

## RESULTS

### Subindices (1–3) resulting from field data

*Microbial mat surface area ($I_A$)*

In February, $I_A$ values for the lower and medium intertidal zone (transect 1) were zero, documenting lack of microbial colonization (Fig. 4). The upper intertidal and lower supratidal zones (transects 1 and 2) were characterized by values ranging from 0·22 to 0·65, representing large microbial mat areas of many m$^2$ extension. At the highest topographic point of transect 2, site X (Fig. 1b), an index of zero was determined.

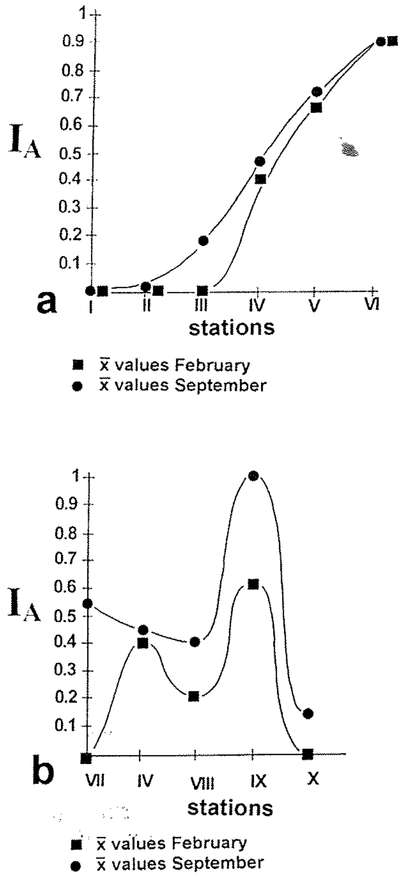

**Fig. 4.** $I_A$ values for investigated stations (roman numbers on $x$-axis). (a) Transect 1: the main seasonal differences in areas covered by mats were found in the medium to upper intertidal zones (stations III–V), whereas the lower intertidal and lower supratidal areas showed similar values. (b) Transect 2: the values for February were always lower than those for September.

In September, a few mat patches of some dm$^2$ extension occurred randomly in the lower intertidal zone (transect 1) and gave rise to very slightly increased index values. With increasing topographic height (transects 1 and 2), the mat patches became larger (several m$^2$) until, in the upper intertidal zone, up to 50–70% of the tidal surface was overgrown by organic layers. High index values exceeding 0·9 were characteristic of the lower supratidal zone, where the coherent microbial layer was perforated by a few erosional depressions of some dm in diameter.

*Steepness of slope angles of erosional remnants ($I_S$)*

In February, $I_S$ values for the lower intertidal zone (transect 1) approached zero (Fig. 5). Average slope angles of 30° to 60° were determined in the upper intertidal zone (transects 1 and 2), represented by indices of 0·34–0·76. The steepest part of the index curve corresponded to this tidal area, and the variability of the measurements was also quite high. In the lower supratidal zone, slope angles ranged from 30° to 90°, which gave rise to the wide spectrum of index numbers.

In September, the lower intertidal zone (transect 1) showed minor elevated surface parts with slope angles typically of 2–5°. The greatest steepness of the index curve corresponded to the medium intertidal zone. The lower supratidal zone (transects 1 and 2) showed an average value close to 1, demonstrating that most slope angles were around 90°.

*Degree of microbial levelling of the rippled sedimentary surface ($I_N$)*

Whereas, in February, no organic infill could be found in the lower intertidal zone (transect 1) (Fig. 6), relict areas of colonization of a few mm to about 0·5 cm occurred at topographically higher places. At site VIII (transect 2), one measurement of about 2 cm was made. The steepest part of the curves (transects 1 and 2) belonged to the transition zone between the upper intertidal and lower supratidal zone, where the thick organic layer produced index values of about 0·6.

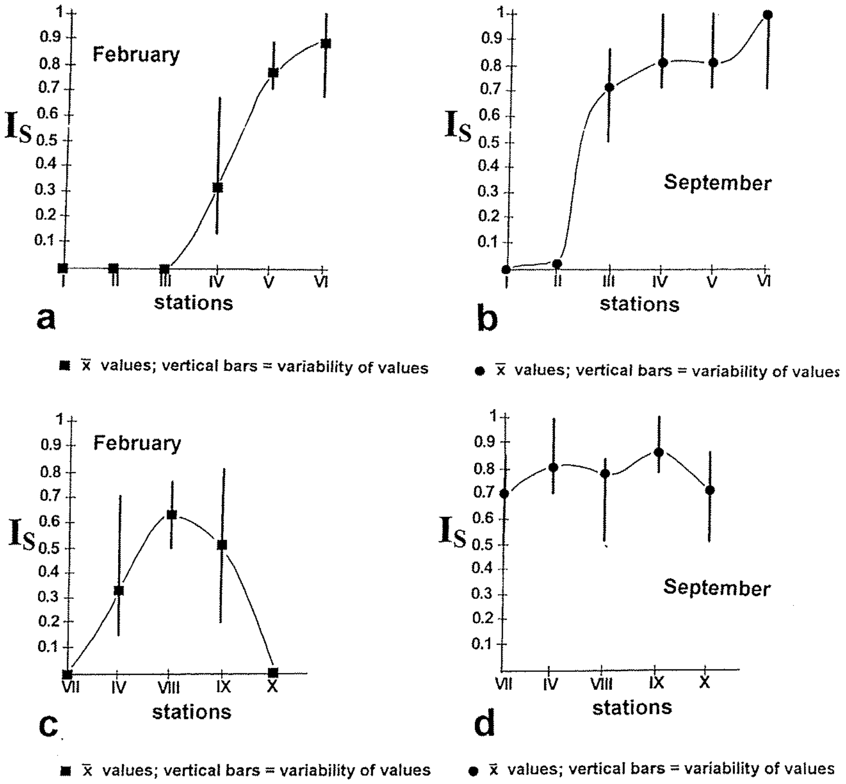

**Fig. 5.** $I_S$ values for investigated stations (roman numbers on $x$-axis). Transect 1: in February (a), the steepest part of the curve represents the upper intertidal zone, whereas in September (b), the steepest inclination characterized the medium intertidal area (stations III and IV). Transect 2: in February (c), relatively high $I_S$ values were determined for the topographically higher parts of the upper intertidal zone (station VIII). In September (d), the numbers at all stations were significant; even maximum values of 1 were determined.

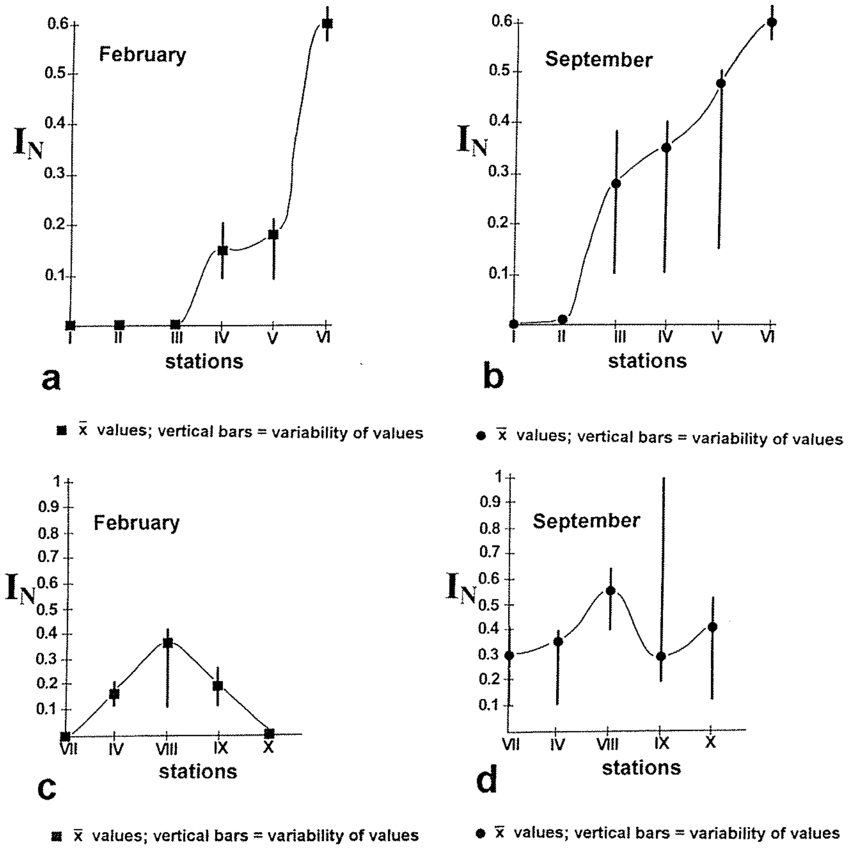

**Fig. 6.** $I_N$ values for investigated stations (roman numbers on $x$-axis). Transect 1: in contrast to the values obtained in February (a), the $I_N$ values for September (b) were significantly higher in the medium to upper intertidal zones (stations III–V). Transect 2: in February (c), the topographically higher parts of the upper intertidal zone showed increased values. The values obtained in September (d) were increased at all stations.

In September, biomass concentrations gave rise to an EPS-rich, cohesive infill of some mm thickness in ripple valleys of the lower intertidal zone (transect 1). The steepest part of the index curve corresponded to the medium intertidal area. Enrichment of sand grains and organic material below the living mat layers of the upper intertidal area (transects 1 and 2) was significantly higher and reached values up to 2·5 cm thick. Maximum index values of up to 1 were found sporadically in the lower supratidal zone of transect 2.

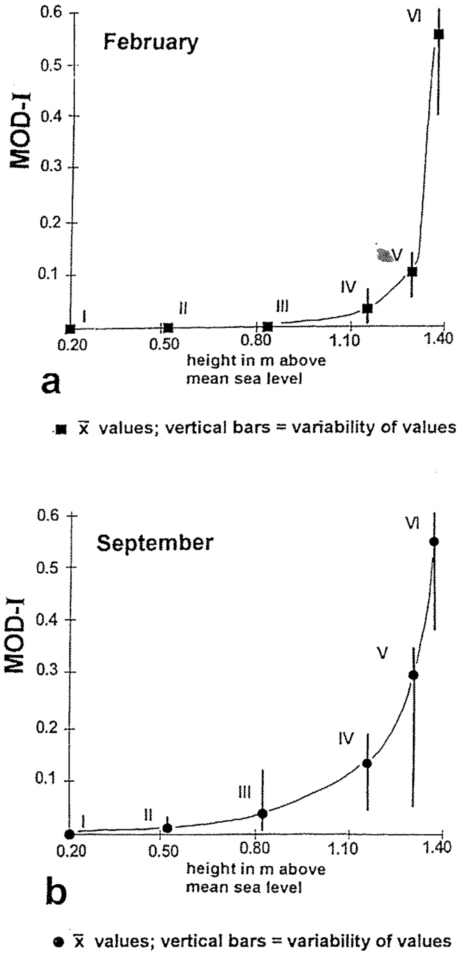

**Fig. 7.** MOD-I values. Transect 1: (a) in February, the values of the lower areas of the tidal flats show no clear microbial influence, whereas the mean value for the lower supratidal zone (station VI) was 0·55. (b) In September, the average MOD-I values were between 0·02 in the lower intertidal and 0·55 in the lower supratidal zones. Both the September and February curves meet at an average index value of about 0·55.

## The modification index (MOD-I) and its application to tidal flat relief

### *Transect 1 (Fig. 7a and b)*

MOD-I values obtained in February in the lower intertidal zone (Fig. 7a) approached zero. In September, however (Fig. 7b), the values were around 0·02 (with low variability) because of slight increases in all subindex numbers.

In contrast, MOD-I values for the lower supratidal zone were relatively high (maximum 0·6), although variable, and did not change significantly between winter and summer. Both the September and February curves overlap at an average value of about 0·55.

The steepest part of the curve corresponded to topographic heights between 1·20 m and 1·40 m above mean sea level.

### *Transect 2 (Fig. 8a and b)*

In February (Fig. 8a), the highest MOD-I value (about 0·1) was determined at about 1·30 m above mean sea level. In this area, MOD-I values increased and reached 0·25 during September (Fig. 8b). Topographically higher sites on the transect reached only an average index of 0·05. As with transect 1, MOD-I values in the upper intertidal area showed greater variability.

## Distribution of cyanobacteria

To evaluate the MOD-I values across transects 1 and 2, the distribution and abundance of the major taxa *Merismopedia punctata, Oscillatoria limosa,* and *Microcoleus chthonoplastes* were recorded (Figs 9 and 10).

In February, *M. punctata* was only present in topographically higher tidal zones. In contrast, in September, this species was distributed from the lower intertidal zone towards the lower supratidal zone of both transects.

*O. limosa* was dominant in the medium and upper intertidal zones. In February, no living specimens of the species were found in the lower intertidal zone (transect 1), although decaying filaments were noted occasionally. In summer, this species extended into the lower intertidal zone, where it mainly colonized elevated surface patches.

*M. chthonoplastes* mainly formed its characteristic tissue-like mats at the mean high water line and in the lower supratidal zone (transects 1 and 2). In February, the mats appeared slightly

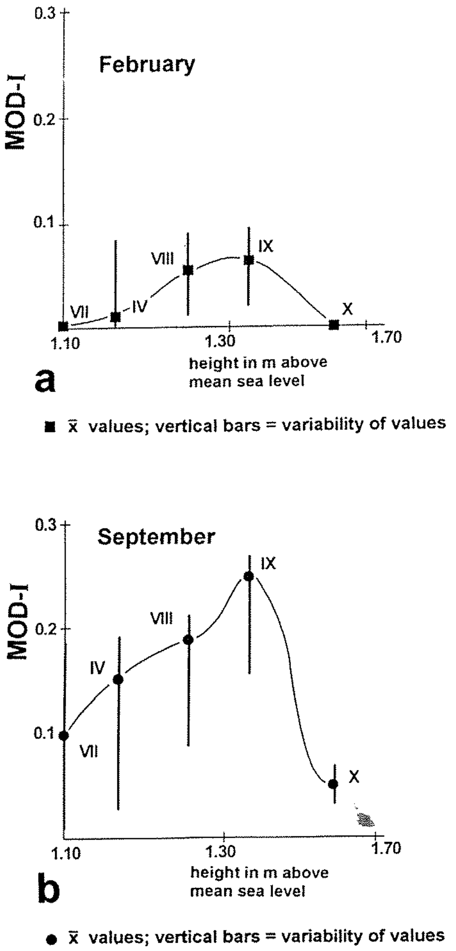

**Fig. 8.** MOD-I values. Transect 2: (a) in February, maximum values of 0·1 characterize station IX, about 1·30 m above mean sea level. In September (b), the station at this topographic height also showed the most significant value.

brownish. Microscopic investigations revealed that, despite the brownish colour of the mat surface, most of the microorganisms were still alive. The colour stemmed from a few degraded cells on the surface. These results corresponded with the high MOD-I value of the lower supratidal zone independent of season. In the lower intertidal zone (transect 1), mats of this species were non-existent.

## DISCUSSION

The lower intertidal zone was characterized by both subindices and MOD-I values approaching zero (Fig. 7a and b). This indicates that biofilms developing in this area did not alter the primary surface relief significantly, even during summer. Owing to significant hydrodynamic forcing at these sites, microbial mats could not develop. Coccoid cyanobacteria (*Merismopedia punctata*) were frequent (Fig. 9b), but did not stabilize the sediments effectively, even if the organisms were able to bind sediment to some extent (Krumbein *et al.*, 1993): *M. punctata* forms cube-like aggregates of cells that cover and glue together individual sand grains of the near-surface sediment. However, coherent mat-secured surfaces did not develop.

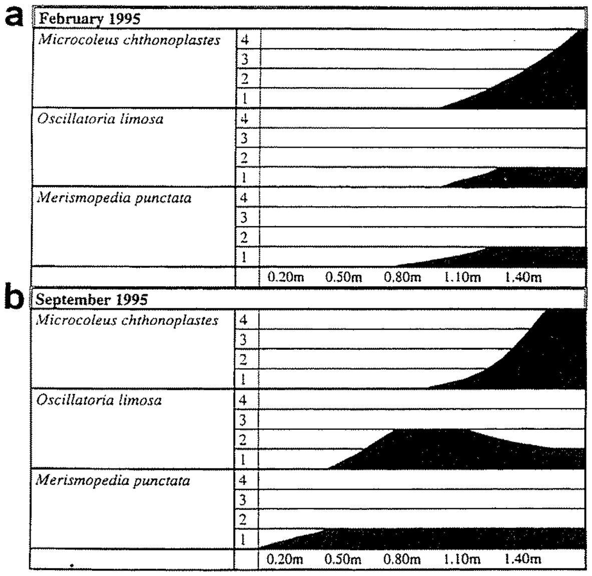

**Fig. 9.** Estimated abundance of major species of mat- and biofilm-forming cyanobacteria across transect 1, evaluated in February (a) and September (b). *x*-axis indicates increasing topographic height from the lower intertidal zone (0·20 m above mean sea level) towards the lower supratidal zone (1·40 m above mean sea level). The abundance was estimated in four ranks: 1, rare; 2, common; 3, frequent; 4, dominant.

Microbial mat development was initiated with the first occurrence of *O. limosa* (Fig. 9b). Although mat-covered surface areas in the lower intertidal zone were very small, the meshwork of the filaments of *O. limosa* effected a higher degree of surface stabilization and levelling. This was documented by slightly increased values for both slope angles (Fig. 5a and b) and surface levelling (Fig. 6a and b) in September. Also, the shape of the subindices and MOD-I curves indicated a microbial influence towards the lower intertidal zone (Fig. 7b). Conversely, the winter measurements (Fig. 7a) showed that the lower intertidal zone was entirely controlled by physical effects.

The medium to upper intertidal zones were characterized by low MOD-I values in winter and relatively high ones in summer (Figs 7 and 8). The same pattern was reflected in all subindex

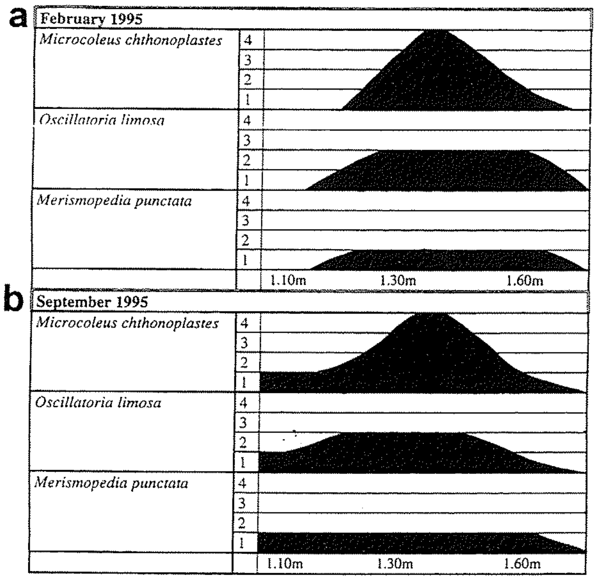

**Fig. 10.** Estimated abundance of major species of mat- and biofilm-forming cyanobacteria across transect 2, evaluated in February (a) and September (b). *x*-axis indicates increasing topographic height from the upper intertidal zone (1·10 m above mean sea level) towards the upper supratidal zone (1·60 m above mean sea level).

values. In these tidal zones, mat development was seasonally controlled. The mats were largely constructed by *O. limosa*, which was able to extend from the lower supratidal into the intertidal zone during summer conditions. *O. limosa* is known for its relatively high mobility and ability to recolonize sandy surfaces immediately after erosion or burial. The spatial distribution of *O. limosa* is also favoured by its ability to fix free nitrogen. Because of these attributes, it is a pioneer species (Stal & Krumbein, 1985; Villbrandt, 1992), forming mats even at sites of higher hydrodynamic stress. As disturbance by hydrodynamic forcing is greater in this topographic zone, the mats showed only a patchy distribution.

*O. limosa* forms single elongated trichomes without an EPS-rich sheath. On account of low EPS, the mats are thin and do not alter the primary physical relief as effectively as do organic layers dominated by *Microcoleus chthonoplastes* (see below).

The high variability of the field measurements and the resulting subindices (Figs 4–6) may reflect the intense interaction between relatively strong erosional and depositional dynamics characterizing this tidal area (low indices) and the rapid microbial adaptation (high indices).

In the lower supratidal zone, non-seasonal variable high MOD-I values obtained from the surface relief indicated the great effectiveness of *M. chthonoplastes* in modifying sedimentary surfaces. Although there is a strong hydrodynamic impact in winter, extended areas of the mat-secured surface were able to withstand erosion. This is documented by $I_A$ values of about 0·9 (Fig. 4). The maximum MOD-I value of 0·6 (Fig. 7) in this zone implies, on the other hand, a still active physical impact (e.g. during spring tides), expressed by erosional pockets. The lower supratidal zone seems to be most favourable for the development of thick microbial mats, because grazing pressure and bioturbation, as well as sedimentation rates are low (Gerdes & Krumbein, 1987). Additionally, the biomass production is increased in places in the lower supratidal zone because of the predominance of *M. chthonoplastes* (Gerdes & Krumbein, 1987). *M. chthonoplastes* usually forms thick bundles of trichomes enclosed by sheaths consisting of EPS, which is very tough and quite resistant to degradation (Decho, 1990). Accumulation of sedimentary particles by trapping and binding is a typical feature associated with this species (Noffke *et al.*, 1997), such that it is particularly involved in levelling formerly rippled sedimentary surfaces (Fig. 6). Besides this, the binding meshwork of thick, EPS-rich bundles effectively interweaves and stabilizes the surfaces of tidal deposits (Neumann *et al.*, 1970; Yallop *et al.*, 1994). At topographically higher sites (Fig. 8) of lower humidity, mat development is greatly reduced, and the organic layers are thin. During winter storms, the mats were largely destroyed.

This study deals with benthic cyanobacterial communities superimposed on the physical background of sandy tidal environments. Accumulation of mineral particles and stabilization effects induced by microorganisms can also be observed in depositional systems of fine-grained sediment, colonized by interfacial, mucus-secreting diatom assemblages (Grant *et al.*, 1986; Black, 1997; Paterson, 1997).

## CONCLUSIONS

The method presented in this paper quantifies different activities of cyanobacteria and their impact on the formation and preservation of sedimentary structures in sandy tidal flats. The method is based on objectively measured field data, and the calculated indices signify the differing ability of changing microbial populations to modify and alter a tidal flat surface. The indices are simple numbers applicable to comparative studies of local and/or temporal influence of microorganisms on sedimentary structures. Whereas biofilms developing in the lower intertidal zone inherit the original shape of the physical sedimentary structures, the increasing abundance of filamentous cyanobacteria modify the structures at topographically higher sites. In the lower supratidal zone, microbial communities have a large impact in modifying surface structures, while physical forces play a minor role.

## ACKNOWLEDGEMENTS

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## REFERENCES

Black, K.S. (1997) Biophysical factors contributing to erosion resistance in natural cohesive sediments. In: *Cohesive Sediments* (Ed. by N. Burt, R. Parker and J. Watts), pp. 231–244, London.

Charaklis, W.G. and Marshall, K.C. (1989) Biofilms: a basis for an interdisciplinary approach. In: *Biofilms* (Ed. by W. G. Charaklis and K. C. Marshall), pp. 1–16. J. Wiley & Sons, New York, Chichester, Brisbane.

De Boer, P.L. (1981) Mechanical effects of microorganisms on intertidal bedform migration. *Sedimentology*, **28**, 129–132.

Decho, A.W. (1990) Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. *Oceanogr. Mar. Biol. Ann. Rev.*, **28**, 73–154.

Gerdes, G. and Krumbein, W.E. (1987) Biolaminated deposits. *Lecture Notes in Earth Sciences*, **9**, Springer, Berlin.

Gerdes, G., Krumbein, W.E. and Reineck, H.E. (1985) Verbreitung und aktuogeologische Bedeutung mariner mikrobieller Matten im Gezeitenbereich der Nordsee. *Facies*, **12**, 75–96.

Gerdes, G., Claes, M., Dunajtschik-Piewak, K., Riege, H., Krumbein, W.E. and Reineck, H.E. (1993) Contribution of microbial mats to sedimentary surface structures. *Facies*, **29**, 61–74.

Grant, J., Bathmann, U.V. and Mills, E.L. (1986) The interaction between benthic diatom films and sediment transport. *Est. Coastal Shelf Sci.*, **23**, 225–238.

Krumbein, W.E. (1983) Stromatolites – the challenge of a term in space and time. *Precambrian Res.*, **20**, 493–531.

Krumbein, W.E., Paterson, D.M., Stal, L.J., *et al.* (1993) Microbially mediated processes in tide influenced deposits and their importance in stabilization and diagenesis of sediments. *Final Rep. EC Mast*, Oldenburg University Press, Oldenburg.

Neu, T.R. (1994) Biofilms and microbial mats. In: *Biostabilization* (Ed. by W. E. Krumbein, D. M. Paterson and L. J. Stal), pp. 9–16. Oldenburg University Press, Oldenburg.

Neumann, A.C., Gebelein, C.D. and Scoffin, T.P. (1970) The composition, structure and erodability of subtidal mats, Abaco, Bahamas. *J. Sedim. Petrol.*, **40**, 274–297.

Noffke, N. (1997) *Mikrobiell induzierte Sedimentstrukturen in siliziklastischen Wattablagerungen.* PhD Thesis, University of Oldenburg.

Noffke, N., Gerdes, G., Klenke, Th. and Krumbein, W.E. (1996) Microbially induced sedimentary structures – examples from modern sediments of siliciclastic tidal flats. *Zbl. Geol. Paläont.*, I, 307–316.

Noffke, N., Gerdes, G., Klenke, Th. and Krumbein, W.E. (1997) A microscopic sedimentary succession of graded sand and microbial mats in modern siliciclastic tidal flats. *Sedim. Geol.*, **110**, 1–6.

Paterson, D.M. (1997) Biological mediation of sediment erodability: ecology and physical dynamics. In: *Cohesive Sediments* (Ed. by N. Burt, R. Parker and J. Watts), pp. 215–229, London.

Paterson, D.M. and Daborn, G.R. (1991) Sediment stabilization by biological action: significance for coastal engineering. In: *Developments in Coastal Engineering* (Ed. by D. H. Peregrine, and J. H. Loveless), pp. 111–119. University of Bristol Press, Bristol.

Reineck, H.E. (1979) Rezente und fossile Algenmatten und Wurzelhorizonte. *Nat. Mus.*, **109**, 290–296.

Riege, H. (1994) *Untersuchungen zur Karbonatfällung in Mikrobenmatten.* PhD Thesis, University of Oldenburg.

Stal, L.J. and Krumbein, W.E. (1985) Isolation and characterization of cyanobacteria from a marine microbial mat. *Bot. Mar.*, **28**, 351–365.

Villbrandt, M. (1992) *Interactions of Nitrogen Fixation and Photosynthesis in Marine Cyanobacterial Mats (Mellum, Southern North Sea).* PhD Thesis, University of Oldenburg.

Wachendörfer, V. (1991) *Parahistologische und sedimentmikrobiologische Untersuchungen an einem potentiellen silikoklastischen Stromatolithen.* PhD Thesis, University of Oldenburg.

Wunderlich, F. (1979) Die Insel Mellum (südliche Nordsee), dynamische Prozese und Sedimentgefüge. I. Südwatt, Übergangszone und Hochfläche. *Senck. Marit.*, **11**, 59–113.

Yallop, M.L., De Winder, B., Paterson, D.M. and Stal, L.J. (1994) Comparative study on primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Est. Coastal Shelf Sci.*, **39**, 565–582.

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