CHANGE OF TOPOGRAPHY AND SEDIMENT CHARACTERISTICS ON AN INTERTIDAL MUD-FLAT FOLLOWING MASS-MORTALITY OF THE AMPHIPOD *COROPHIUM VOLUTATOR*

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A *Corophium*-bed characterized by a mosaic of emerged areas and tidal pools during low water was established on an intertidal flat in the southern part of the Danish Wadden Sea. In spring 1990, the plateaux harboured relatively high densities of the amphipod *Corophium volutator*, whereas the amphipods were almost absent in the pools. Following a parasite-induced mass-mortality in the population of *Corophium*, summer 1990, the plateaux of the bed were subjected to sediment erosion. The heterogeneous plateau-pool structure disappeared, accompanied by increased median particle diameter and decreased silt content in the former plateau sediment. These events were accompanied by increased chlorophyll-*a* concentrations in the sediment of both plateau and pool areas.

The results suggest *Corophium volutator* to be the single most important organism stabilizing the plateau sediment, and hence, the heterogeneous topographic structure of the *Corophium*-bed. It is proposed that the stabilizing effect of *Corophium* burrows also in deeper sediment strata may outweigh the surface stabilizing influence of epipellic diatoms, as well as the negative effect of amphipods eating the diatoms, in non-cohesive coarser sediments.

INTRODUCTION

Many studies have been devoted to the identification of factors and processes influencing sedimentation and resuspension of particles in coastal waters (see references below). These have been initiated by the increase of human activities in such areas (e.g. construction of harbours, dykes, bridges, channels etc.), and also by marine ecologists studying the structure and development of benthic plant and animal communities. Both the human activities and the benthic communities may affect, or may themselves be affected by, sedimentation and erosion processes on the sea-bottom. Also, awareness of post-glacial coastal sinking in certain regions of the world and the expected rise in sea level due to global warming (both probably changing the hydrodynamic properties of near-coastal waters) may in the context of e.g. coastal protection have reinforced the interest into factors affecting the stability of marine sediments.

Beside the obvious influence of hydrodynamic forces and the particle composition of the substrate itself (e.g. McLusky, 1989), biotic processes may affect significantly the stability of marine sediments (Gray, 1974; Rhoads & Boyer, 1982; Grant, 1988; Vos et al., 1988; Heinzelmann & Wallisch, 1991; Miller et al., 1996). It appears that benthic microalgae are important sediment stabilizing organisms (see Holland et al., 1974; Coles, 1979; de Boer, 1981; Grant et al., 1986; Grant, 1988; Vos et al., 1988; Paterson, 1989; Heinzelmann & Wallisch, 1991; Madsen et al., 1993; Underwood & Paterson, 1993a,b; Gerdol & Hughes, 1994a; Yallop et al., 1994). This applies especially to the epipellic diatoms that during their movements in the upper sediment strata produce extracellular mucopolysaccharides which bind the sediment particles together (e.g. Edgar & Pickett-Heaps, 1984).

The effect of infaunal macroinvertebrates on sediment stability, in contrast, is considerably more ambiguous. Some species are reported to destabilize the substrate causing erosion (Rhoads & Young, 1970; Eckman et al., 1981; Nowell et al., 1981; Rhoads & Boyer, 1982; Luckenbach, 1986; Jones & Jago, 1993; Gerdol & Hughes, 1994a), whereas others apparently stabilize the sediment and/or cause increased sedimentation (Fager, 1964; Mills, 1967; Young & Rhoads, 1971; Daro & Polk, 1973; Myers, 1977; Rhoads & Boyer, 1982; Meadows & Tait, 1989; Meadows et al., 1990; Jones & Jago, 1993). And even within species there may be a functional difference depending on the actual density of the animals (see Eckman et al., 1981; Grant & Daborn, 1994).

Although most studies attempt to elucidate the direct influence of a single organism or a group of organisms on sediment stability, some also consider the influence of the dynamic interplay between benthic diatoms and the herbivorous infauna. Benthic animals feeding on, and thereby depressing the population of, the stabilizing microalgae must indirectly destabilize the substrate. Hence, removal of the infauna using various chemicals has demonstrated an increase in the population of diatoms accompanied by increased sediment stability or sediment deposition (Coles, 1979; Gerdol & Hughes, 1994a). Of particular interest in this context is the tube-dwelling amphipod *Corophium volutator* (Pallas) which may occur in densities exceeding 100,000 ind m⁻² (Mouritsen, 1994; Gerdol & Hughes, 1994a). Through their substantial impact on the population of benthic diatoms (Hawkins, 1985; Gerdol & Hughes, 1994b), these amphipods are usually considered as sediment destabilizers (Coles, 1979; Daborn et al., 1993; Gerdol & Hughes, 1994a). However, Meadows & Tait (1989) and Meadows et al. (1990) have presented contradictory evidence showing that *C. volutator* is also able to stabilize the substrate directly through compaction of the sediment and secretion of mucous during tube-building (see also Grant & Daborn, 1994). Since *C. volutator* is a significant macrofaunal organism in the intertidal soft-bottom ecosystem, often showing large and erratic fluctuations in densities (Reise, 1978; Fish & Mills, 1979; Möller & Rosenberg, 1982; Murdock et al., 1986; Olafsson & Persson, 1986; Matthews et al., 1992; Flach, 1996), it is of importance to unravel the role of this species for the stability of intertidal sediments.

Through the analysis of field data collected during a period of total disappearance of a *Corophium*-bed, this paper aims to illustrate that *Corophium volutator* under certain conditions may stabilize intertidal sediments.

MATERIALS AND METHODS

The study site

The study site was located 600 m seaward from the mean high water level (MHWL) on a 1500 m wide intertidal zone in the southern part of the Danish Wadden Sea (Højer tidal flat, 54°56'N 08°39'E). Close to the MHWL of this mud-flat, a dyke was constructed in 1981. In front of the dyke, silty trenches were established from about MHWL to 200 m in the seaward direction.

At least from autumn 1989 and until present time, an area between 100 and 800 m seaward from MHWL (embracing the main study site) has been characterized by a well-developed *Corophium*-bed, composed of a mosaic of emerged soft-sediment plateaux and tidal pools during low water (Figure 1A). In 1990 the bed covered an area of 80 ha, whereas the bed-structure was present at least along a 5 km shoreline in 1996. Based on a transect-survey carried out at maximum low water at the study site in September 1989, the plateaux made up 56% of the bed-area and measured 3.7 ± 0.5 m in diameter (mean $\pm$ SE, N=227). The maximum water depth in the pools was 3.8 ± 0.1 cm (N=104), and the difference in level between the top of the plateaux and the lowest part of the pools was measured to be 5.7 ± 0.4 cm (N=10).

Based on visual/manual inspection of the bed sediment, it is evident that the plateaux support high densities of *Corophium volutator*, and that the sediment is well-oxidized, very soft and 'cohesive' down to a depth of 5–6 cm. This description forms a

Figure 1. Photographs of the *Corophium*-bed area taken in a shoreward direction. (A) The well-developed bed in September 1989 showing the mosaic of plateaux and pools. (B) The same area as it appeared in October 1990. Unfortunately, no photographs from summer 1990 were available. However, disregarding the sand ripples in the October photograph the overall impression of a topographically homogeneous intertidal flat was similar to the situation in July and August 1990.

contrast to the situation in the tidal pools where rather few amphipods are established in a relatively hard and less 'cohesive' substrate having an oxidized zone of only 1–2 cm.

The data originate from sampling of the *Corophium*-bed on five occasions in 1990 (13 March, 5 May, 12 June, 18 July and 22 August), if not otherwise mentioned. We will, however, refer extensively also to other visits at the study site especially regarding the development of the topographic structure of the bed.

Sampling of macrofauna

On each sampling occasion, one core sample (50 cm², 25 cm deep) was taken from each of ten plateaux and ten tidal pools. On 18 July, however, only seven instead of ten samples were taken from the pools. The sediment cores were sieved in the field through a 500- μ m mesh and retained animals were preserved in 4% formaldehyde. In the laboratory, all macrofaunal specimens were counted and, regarding *C. volutator*, measured (rostrum to telson) under a stereomicroscope.

Chlorophyll-a measurements

In order to estimate the abundance of benthic microalgae, one core sample of the upper sediment strata (5 cm², 3 cm deep) was collected on five plateaux and in five pools at each visit between May and August (on 18 July, however, only three instead of five samples were taken in the pools). The sediment cores were stored in a freezer (-18°C) until further treatment. To determine the chlorophyll-*a* concentrations, 10 g homogenized sediment from each sample was added to flasks containing 30 ml 96% ethanol. The flasks were placed in darkness in a shaker for 12 h at room temperature, 10 ml of the ethanol with extracted chlorophyll was subsequently centrifuged for 10 min (3000 rpm) and the chlorophyll-*a* concentration was then determined spectrophotometrically following the method of Lorentzen (1967).

Chlorophyll-*a* concentrations are not necessarily direct measures of the population of benthic diatoms. However, on the upper zone of intertidal mud-flats they usually are (Admiraal, 1984; Paterson et al., 1990; Underwood & Paterson, 1993a,b; Yallop et al., 1994), and although there is no quantitative data on the species composition of benthic microalgae from the study site, qualitative inspections of the sediment (using light microscopy) have revealed dominance of large epipelagic diatoms. It is therefore assumed that the chlorophyll-*a* concentrations in the present study are estimates of the population of benthic diatoms.

Sediment penetrability

The penetrability of the substrate on plateaux and in pools was recorded in May and August by using a penetrometer designed in the laboratory. A conical steel rod (12.0 cm long, 0.2–1.0 cm diameter, 61.3 g) with scale markings was dropped from a standard height (180 cm) through a tube mounted on a stand. Penetrability was measured as the distance (cm) the cone penetrated the substrate. A high score indicated highly penetrable (soft) sediment.

Sediment composition

From 5 May and onwards, one additional sediment core (24 cm², 3 cm deep) was taken from three plateaux and three pools. The samples were subsequently separated into particle fractions (particle size > 1000, 500, 250, 125, 63 μ m, and < 63 μ m) by wet-sieving. The ash-weight of the dried sediment fractions were determined after 24 h at 520°C. From these data the median particle diameter and silt content (the proportion of particles [dw/dw] < 63 μ m in diameter) were calculated for each sediment sample.

Measurements of net sedimentation

The net sedimentation on plateaux and in pools was measured using a direct method. Pairs of wooden sticks (1.2 m in height, 2.5 cm in diameter), 4 m apart, were pushed 60–70 cm into the substrate on 5 May and left there during the course of the study. At the subsequent visit in June and August, a nylon string was tightly stretched out between the wooden sticks, and the distance between the string and the sediment surface was measured. Such pairs of wooden sticks were established in connection to nine plateaux (N=9 at each visit). In the tidal pools, measurements were carried out in a similar way, but since an accurate determination of the sediment surface was difficult because of the presence of water, the distance measured was between the string and a short quadrangular wooden stick placed temporarily on the sediment surface of the pools. In these pools eight measurements were obtained in May and June, whereas only six measurements were obtained in August.

Sampling following the disappearance of the bed-topography

Although the plateau-pool structure of the bed disappeared during summer 1990 (see below), it was still possible to continue sampling on former plateau and pool areas, separately. Based on the known position of the wooden sticks previously placed on plateaux and in pools, it was evident that these areas both in July and August still maintained their respectively 'soft' and 'hard' substrates. This could be assessed by walking on the sediment. Measurements of sediment penetrability (see Results) also indicate a resemblance between plateau and 'soft' substrate as well as between pool and 'hard' substrate.

Statistical analysis

Statistical tests were performed using Statistical Package of Social Science (SPSS) (Hull & Nie, 1981). All parametric tests were preceded by tests for assumptions (normal distribution and homogeneity of variance). Where these assumptions were violated non-parametric statistics were applied. Although median and range may be more appropriate descriptive statistics when non-parametric analysis are used, mean values and standard errors (SE) are nevertheless given as default values throughout the paper. Pair-wise comparisons following main analyses (ANOVA or Kruskal-Wallis test) were carried out only orthogonally.

RESULTS

Topographic changes of the bed: qualitative description

The *Corophium*-bed was discovered in September 1989. At that time, the topographic structure of the bed was very well-developed (Figure 1A), and the plateaux supported high densities of *Corophium volutator* ($>100,000$ ind m^{-2} ; Mouritsen, 1994). The characteristic bed-topography persisted during the following winter (data not shown) and spring until sampling on 12 June. At the subsequent visit in July, however, the former plateau-pool structure had vanished completely seaward from the silty trenches. Visual signs of the usual topography of the bed could no longer be found (Figure 1B). Within the silty trenches, in contrast, the *Corophium*-bed was still present. This pattern persisted more or less until April 1991 where the former bed-area began to regain its previous topography.

Major macrofaunal changes

As judged by their abundance, the amphipod *C. volutator* and the mud snail *Hydrobia ulvae* were the single most important macrofaunal organisms present on the main study site. The amphipods showed during March and May a very significant pattern of spatial distribution with much higher densities on plateaux than in pools (Figure 2). From May to June, however, the entire population of *C. volutator* vanished from the main study site and did not recover during 1990. Based on the samples taken in the silty trenches in July, the amphipods persisted here with an average density of $30,220 \pm 7443$ specimens m^{-2} on the plateaux and 140 ± 79 ind m^{-2} in the pools.

Figure 2. Temporal changes in the density of *Corophium volutator* (mean number $m^{-2} \pm SE$) on the plateaux (●) and in the pools (○) from the main study site. The abundance of amphipods decreased significantly both on the plateaux (Kruskal-Wallis test: $\chi^2=40.92$, $N=50$, $P<0.001$; ***, Mann-Whitney test: $Z=-3.72$, $N=20$, $P<0.001$) and in the pools (Kruskal-Wallis test: $\chi^2=23.69$, $N=47$, $P<0.001$; **, Mann-Whitney test: $Z=-3.11$, $N=20$, $P<0.001$). Orthogonal comparisons other than those marked by asterisks were not significant (Mann-Whitney tests: $P>0.14$).

In May, the size–frequency distribution of the amphipods was bimodal, with a juvenile and an adult cohort measuring on average 2–3 mm and 7–8 mm in length, respectively. The proportion of juveniles and adults was almost similar (see Jensen & Mouritsen, 1992 for details).

The density of mud snails also showed some temporal changes both on plateaux (one-way ANOVA: $F_{4,49}=12.07$, $P<0.001$) and in pools ($F_{4,46}=8.02$, $P<0.001$). These changes were (at least proportionally) less dramatic as in the amphipods, showing fluctuations in densities between ~15,000 and 28,000 *Hydrobia* ind m^{-2} from March to August. The most interesting change was seen during the disappearance of the bed-topography between May and June. Here the density of *H. ulvae* dropped significantly from ~24,000 to 16,000 ind m^{-2} on the plateaux (LSD a posteriori test: $P<0.05$). The mud snails were contrary to the amphipods few in numbers in the silty trenches, with mean densities of 920 ± 200 ind m^{-2} on plateaux and 1300 ± 336 ind m^{-2} in pools.

On the main study site, other macrofaunal organisms occurred in densities one to three orders of magnitude less than amphipods and snails (May densities), and were considered of minor importance in the present context. The seasonal change in abundance of these animals (mainly *Tubificoides benedeni*, *Heteromastus filiformis*, *Nereis (Hediste) diversicolor*, *Pygospio elegans*, and juvenile *Macoma balthica*) is presented elsewhere (Jensen & Mouritsen, 1992).

Changes in chlorophyll-a

The chlorophyll-*a* concentrations in the sediment showed significant changes between May and August both on the plateaux (one-way ANOVA: $F_{3,16}=9.31$, $P<0.001$) and in the pools ($F_{3,14}=17.84$, $P<0.001$) (Figure 3A). Least Square Difference pair-wise a posteriori tests revealed that this was due to a significant increase in chlorophyll concentrations between May and June on both sites ($P<0.05$). Despite the slight decrease from June to August on the plateaux, the overall development in chlorophyll-*a* concentrations on plateaux and in pools was similar.

Changes of sedimentological properties

Penetrability

In May the penetrability of the plateau sediment was significantly higher (6.6 ± 0.2 cm, $N=30$) than the pool sediment (5.3 ± 0.1 cm, $N=30$; Mann–Whitney test: $Z=-5.04$, $P<0.001$). A similar result was obtained when comparing soft (former plateau) sediment (6.4 ± 0.2 cm, $N=10$) and hard (former pool) sediment (5.0 ± 0.1 cm, $N=10$; Mann–Whitney test: $Z=-3.59$, $P<0.001$) in August. The small numerical reduction in penetrability scores on both soft and hard substrate from May to August was non-significant (Mann–Whitney test: $Z>-1.56$, $P>0.12$). Hence, guided by the position of the wooden sticks and our qualitative impression of the consistency of the substrate, we are confident that both July and August sampling was carried out in former plateau and pool areas, separately.

Figure 3. Changes in sediment characteristics from May to August 1990 on the main study site (plateaux: ●; pools: ○). (A) Chlorophyll-*a* concentrations in the upper sediment strata (mean $\mu\text{g cm}^{-2} \pm \text{SE}$). *, LSD a posteriori test: $P < 0.05$. (B) Silt content (mean % [dw/dw] $\pm \text{SE}$). **, LSD a posteriori test: $P < 0.01$. (C) Net sediment deposition (mean mm $\pm \text{SE}$). Orthogonal pair-wise comparisons other than those marked by asterisks (A & B, only) were not significant (LSD a posteriori tests: $P > 0.05$).

Silt content

Prior to the disappearance of the *Corophium*-bed, the silt content of the sediment on plateaux was significantly higher (12%) than in pools (9.5%; Mann-Whitney test: $Z = -1.96$, $P = 0.0495$) (Figure 3B). Later, however, the silt content in both plateau and pool sediment decreased significantly (one-way ANOVA: plateaux, $F_{3,11} = 7.13$, $P = 0.012$; pools, $F_{3,11} = 4.52$, $P = 0.039$) to a common level of ~8.5% in August (Mann-Whitney test: $Z = -0.66$, $P = 0.51$). The decline in silt content was evident between June and July on the plateaux, whereas in the pools it decreased significantly between July and August (see Figure 3B; LSD a posteriori tests: $P < 0.01$).

Median particle diameter

The changes in silt content were naturally accompanied also by changes in the median particle diameter (MPD) of the substrate. On the plateaux, the MPD increased significantly from 0.102 ± 0.004 mm in May to 0.120 ± 0.002 mm in July (one-way ANOVA: $F_{3,11}=6.95$, $P=0.013$; LSD a posteriori tests: $P<0.05$). In the August samples, however, the MPD had again decreased somewhat (0.108 ± 0.003 mm). The MPD of the pool sediment varied between 0.101 and 0.110 mm from May to August. The largest numerical changes was an increase from 0.101 ± 0.0006 mm in July to 0.110 ± 0.007 mm in August, during which period also the silt content of the sediment decreased. However, none of the changes in MPD from the pool sediment can be considered statistically significant (Kruskal-Wallis test: $\chi^2=6.74$, $N=12$, $P=0.081$).

The studied sediment may be defined formally as non-cohesive fine sand, because of the rather low silt content and a MPD between 0.10 and 0.12 mm.

Sedimentation

From May to August, there was a significant erosion of the plateau sediment (Mann-Whitney test: $Z=-2.74$, $P=0.006$) accompanied by a significant deposition of sediment in the pool areas (Mann-Whitney test: $Z=-3.10$, $P=0.002$) (Figure 3C).

DISCUSSION

The present results indicate that *Corophium volutator* may be the single most important organism responsible for the stability of the plateau sediment. During or following the disappearance of the amphipods, the plateaux were subjected to erosion accompanied by a decrease in the silt content and an increase of the median particle diameter (MPD) in the remaining substrate. Following the equalization of the heterogeneous bed topography, possibly caused both by erosion of the plateaux and sedimentation in the pool areas, the smallest particle fraction also in the former pool areas began to disappear. The result was a homogeneous mud-flat in August where both the silt content and the MPD was quite similar between the former plateau and pool areas.

Further evidence supporting amphipods as the main agent stabilizing the plateau sediment, is provided by the data from the silty trenches that may serve as a control. Within these trenches, positioned just 400 m shoreward to the main study site, not only the *Corophium* population but also the bed topography persisted. We acknowledge, however, that data from the silty trenches can not be considered a true control because the hydrodynamic forces here may depart somewhat from the situation at the main study site.

The sudden disappearance of the amphipods from the main study site in 1990, can be ascribed to parasite-induced mass-mortality as reported elsewhere (Jensen & Mouritsen, 1992; Mouritsen & Jensen, 1997). Hence, the present results parallel the work by Daborn et al. (1993) who argued that migratory shorebirds through their predation on an intertidal population of *C. volutator* in Minas Basin, Canada, caused an increase in the abundance of benthic microalgae. This, in turn, increased the

stability of the sediment. On Højer tidal flat, this 'ecological cascade effect' was instead initiated by the parasites causing a decline in the population of amphipods as well, but with the exact opposite result: a destabilization of the substrate.

In agreement with Daborn et al. (1993), two other field studies on the effect of *C. volutator* on sediment stability (Coles, 1979; Gerdol & Hughes, 1994a) have, through experimental removal of the amphipods by chemicals, demonstrated an increase in the abundance of microalgae in the treated areas followed by increased sediment deposition or stability. In the present study, the population of benthic microalgae also increased rapidly during the disappearance of the amphipods, but did so both on plateaux and in pools (see Figures 2 & 3A). Firstly, this demonstrates that the destabilization of the plateau sediment is unrelated to the population dynamics of the otherwise stabilizing benthic microalgae, and hence, further indicates amphipods as the important sediment stabilizing organism. Secondly, it demonstrates that the observed increase in the abundance of phytobenthos (expressed as chlorophyll-*a* concentrations) from May to June is unrelated to the disappearance of the amphipod grazers. This is because the chlorophyll-*a* concentrations increased rapidly both on the plateaux and in the pools albeit these two habitats previously supported very different amphipod densities of ~14,000 ind m⁻² and none, respectively. Also *Hydrobia ulvae*, however, are important grazers on benthic microalgae (Jensen & Siegismund, 1980). Because these quite abundant gastropods decrease in densities (at least on the plateaux) from May to June, their decline may be an additional factor causing the population of microalgae to increase. However, epipellic diatoms may also be involved in actual blooms on intertidal flats, especially during the summer months (Underwood & Paterson, 1993b; MacIntyre et al., 1996, and references therein). We propose the latter to be the most simple and consistent explanation for the similar increase of chlorophyll-*a* concentrations in the two different microhabitats.

The mechanism behind the sediment stabilizing role of *C. volutator* can be inferred from Meadows & Tait (1989) and Meadows et al. (1990). During tube-building, these amphipods secrete mucous-like material that binds the sediment particles together and thereby increase the shear strength of the substrate. Since *C. volutator* makes 4–5 cm deep burrows (Jensen & Kristensen, 1990), these animals may stabilize the sediment down to a depth of several centimetres. Benthic diatoms, in contrast, are mainly restricted to the upper few millimetres of the substrate (Yallop et al., 1994; MacIntyre et al., 1996, and references therein). So, intertidal sediments stabilized primarily by epipellic diatoms may be vulnerable to strong hydrodynamic forces, such as onshore storms. Once the upper millimetres of the sediment are removed, the underlying substrate is open for rapid erosion (Miller et al., 1996). Severe meteorological conditions usually result in major erosion of coastal sediments (Dolan et al., 1990). However, the plateaux of the presently studied *Corophium*-bed persisted e.g. during an onshore hurricane force storm occurring in January 1990 (see Maddox, 1990), but disappeared several months later during relatively calm weather conditions. Data from a meteorological station nearby the study site showed the occurrence of onshore winds (wind directions between south-west and north-west) during 47 d from 1 January to 12 June 1990 (37 d with an average wind speed between 10 and 15 m s⁻¹, 7 d between 15 and 20 m s⁻¹, and 3 d above 20 m s⁻¹). In contrast,

between 12 June and 18 July during which period the *Corophium*-bed disappeared, the only stronger onshore winds recorded were 7 d with wind speeds between 10 and 15 m s⁻¹. Hence, the ability of the bed to resist strong hydrodynamic forces was considerably better prior to than following the disappearance of the amphipods. This extraordinary resistance of the bed against strong hydrodynamic forces may be explained by the amphipods ability to stabilize the sediment. An additional factor may be a stabilizing compaction of the sediment caused in part by drying out of the plateau substrate during low water (see Paterson et al., 1990), and in part by the amphipods themselves (see Meadows & Tait, 1989). Nevertheless, since the chlorophyll-*a* concentrations measured in the bed sediment during summer 1990 correspond to values previously reported to increase the stability of intertidal sediments (Daborn et al., 1993; Gerdol & Hughes, 1994a), the sediment stabilizing property of the amphipods seems to override any similar effect of benthic microalgae at our study site.

Although details on particle size distribution often are missing, it is our impression that many studies showing stabilizing effects of microalgae were carried out on sheltered mud-flats characterized by cohesive silty substrates. In such habitats the binding property of epipellic diatoms may be identified as the most important factor for sediment stability because the influence of e.g. *Corophium* burrows in deeper sediment strata is rarely tested. On a relatively more wave-exposed tidal flat with coarser non-cohesive sediments as in the present study, the stabilizing effect in the depth of *Corophium* burrows may outweigh the direct influence of diatoms as well as the indirect negative effect of amphipods eating these diatoms.

The penetrability of sediments inhabited by the amphipods (plateaux) was significantly higher than in sediments without amphipods. Since sediment penetrability is often considered negatively related to the shear strength of the substrate, it may be argued that the plateaux were more erodible than the pool sediment, and in turn, that the presence of *Corophium* increased erosion rather than stability. We do not, however, acknowledge sediment penetrability as a single unifying estimate of sediment stability unless the influence of other physical properties of the sediment and the abundance of tube-building macrofauna are considered very carefully. A substantial part of the plateau sediment was occupied by *Corophium* burrows (=water or air during low water). It is therefore to be expected that a penetrating steel cone (with dimensions like ours) can displace an amphipod rich substrate with great ease, and hence, give rise to high penetrability scores. Such measures, however, may be entirely unrelated to the resistance of the sediment to hydrodynamic erosion, if a larger part of the sediment particles are embedded in an adherent matrix of e.g. animal made mucous.

In concert with the laboratory work by Meadows & Tait (1989), Meadows et al. (1990), and Grant & Daborn (1994), the present results indicate *C. volutator* to be a potentially important sediment stabilizing organism on intertidal flats. This picture is, however, contradicted by the field studies of Coles (1979), Daborn et al. (1993) and Gerdol & Hughes (1994a). Since these and the present study are carried out on different mud-flats, characterized no doubt by different abiotic conditions (e.g. hydrodynamic forces, amount of suspended particles in the tidal current, sediment

particle composition, topography etc.), this may not be surprising. Nevertheless, the equivocal evidence on the sediment stabilizing role of *C. volutator* indicates a requirement for more studies.

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