

## Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea

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### Abstract

Macrozoobenthic communities within and outside of the drift algal mats were compared in Kõiguste Bay, NE Baltic Sea. The patches of the drift algae were on average 0.5–1 km wide in diameter covering about 25% of the total bottom area of the bay. Thickness of the mat did not exceed 6 cm. The biomass of the mat varied between 35 and 1391 g dw m<sup>-2</sup>. The drift algal mats had no clear negative effect on macrozoobenthos except for a few infaunal species. The drift algae favoured several detritivorous, herbivorous and carnivorous species. Among the studied variables, the thickness of algal mat and oxygen concentration at near-bottom layer explained the best the structure of macrozoobenthos. Total number of invertebrate species increased curvilinearly with the thickness of algal mat having the peak value at 3–5 cm thick algal mat. To conclude, moderate drift algal mats increased habitat complexity and, thus, the diversity of benthic faunal assemblages in otherwise poorly vegetated coastal areas.

### Introduction

During the last decades excessive growth of opportunistic macroalgae has become a worldwide phenomenon (e.g. Morand & Briand, 1996) including the Baltic Sea (Schramm, 1996; Bonsdorff et al., 1997; Bäck et al., 2000; Norkko et al., 2000; Vahteri et al., 2000; Lehvo & Bäck, 2001; Berglund et al., 2003; Martin et al., 2003). The macroalgal blooms have been associated with an increased nutrient loading of coastal sea areas as the algae that are involved in blooming events are filamentous or laminar forms with high growth and nutrient uptake rates (Duarte, 1995; Valiela et al., 1997). The algal mats form in shallow areas and may later accumulate in deeper zones (Fletcher, 1996; Morand & Briand, 1996; Valiela et al., 1997). In the Baltic Sea they may be more than a meter thick, cover an area of several hectares and usually become totally anoxic at later stages (Vahteri et al., 2000).

The actual impact of the algal mat on benthic invertebrates is largely unpredictable. The disturbance of zoobenthos at the community level may be moderate (Everett, 1994) but likewise a breakdown of communities might occur (Norkko & Bonsdorff, 1996a). The positive effects of the algal mats are the increased food resources either for herbivores (Norkko et al., 2000; Cardoso et al., 2002) or detritivores (Norkko & Bonsdorff, 1996b, c; Renaud et al., 1999), higher dispersal efficiency (Ingólfsson, 1998; Brooks & Bell, 2001) or refuge from predators (Norkko, 1997; Aarnio & Mattila, 2000). The negative effects are increased stress due to hypoxia, especially for groups of limited mobility (Everett, 1994; Norkko & Bonsdorff, 1996a, b), reduced escape from predators (Norkko & Bonsdorff, 1996b) but probably lower predation efficiency (Tallqvist et al., 1999). In general thick and uniform mats disturb zoobenthos more than the patchy drift algae but the nature of the impact is highly species specific. When drifting algae are

abundant a periodic oxygen deficiency develops in sediments below the mat causing impoverishment of zoobenthic communities. On the other hand, under the thin and patchy algal mat oxygen conditions are likely not affecting invertebrate populations. Instead, the algae may provide invertebrates better habitat and food conditions than in unvegetated bottoms. The algal decomposition, attractiveness and edibility differ among species (Heckscher et al., 1996; Peckol & Rivers, 1996; Kotta et al., 2000; Paalme et al., 2002). Therefore, there is a need for field observations where the structure of drift algae and macrozoobenthic communities are compared taking into account other environmental variables such as oxygen content, sediment type and the presence of attached macroalgal assemblages.

In the present study the influence of drift algal mats on the structure of macrozoobenthic community was evaluated in Kõiguste Bay, NE Baltic Sea. Zoobenthos assemblages within the algal mat were compared with the fauna of adjacent mat-free area. The most important species contributing to differences between communities were determined. It was assumed that owing to hypoxic events in sediment the infaunal communities should have low diversity and high share of mobile species. The animals of limited mobility, including the keystone species *Macoma balthica* (L.), are likely depressed. On the other hand, mobile herbivorous and detritivorous species gain from an additional food source, and their densities are higher in the drift algae as compared with the adjacent sea.

## Materials and methods

The study was conducted in the shallow semi-enclosed Kõiguste Bay, Gulf of Riga, NE Baltic Sea (58°22' N, 22°58' E). The prevailing sediment types of the bay are sandy clay mixed with pebbles, gravel or boulders. The area is influenced by a diffuse nutrient load from the moderately eutrophicated Gulf of Riga (Astok et al., 1999). Extensive proliferation of ephemeral macroalgae and the appearance of drift algal mats have been reported from the area in the recent years (Kotta et al., 2000; Paalme et al., 2002; Martin et al., 2003). The drift algae appear in late May. The algal mats persist almost in the same

location in June–July due to the prevailing calm weather conditions and moderate exposure. The drift algae disappear in August (Paalme et al., 2004). In the present study, the patches of the drift algae were on average 0.5–1 km wide in diameter covering about 25% of the total bottom area of the bay. Thickness of the algal mat ranged from 1 to 6 cm. Algal coverage was 100%, with a patchy zone of 2–3 m width along the edges of the mat. The coverage and biomass of attached macrophytes were low in the study area.

The samples were collected by a diver along two 1 km long transects in June–July 2000, 2002 and 2003. Transects were situated perpendicular to the shore between 3 and 5 m depth. The distance between transects was 1 km. Both transects crossed algal mats and unvegetated bottom habitats. Five sampling sites were located at an almost unvegetated bottom and seven sites in the area covered by an algal mat. Altogether 36 samples were taken. The unvegetated sites were situated more than 100 m from the edge of the mat. Owing to stability of the algal mat (Paalme et al., 2004) those areas were not temporally covered by the drift algae. Sediment and macroalgae were collected with Tvärminne core sampler (surface area 315 cm<sup>2</sup>, sampled sediment layer 15 cm) (Kangas, 1972). Before sieving, the samples were split into two parts in order to better distinct infauna and the species associated to algal mat. The layer of the drift algae was gently separated from the remaining sample by cutting the sample at water-sediment interface by small plastic spade. Care was taken not to resuspend the sediment. Samples were sieved with a 0.25 mm mesh and frozen at –20 °C.

During sampling the sediment type, depth, coverage of phytobenthos, dominant species and thickness of algal canopy were recorded. The concentration of oxygen at the sediment surface was measured with an oxymeter OXY 92. In the laboratory all samples were sorted under a binocular microscope (20–40× magnification). All species were determined to the species level except for oligochaetes, chironomids and juveniles of gammarid amphipods. Individuals of all taxa were counted and weighed. Prior to weighing animals were dried at 60 °C for 48 h and plants for 2 weeks, respectively.

The effect of the algal mat on the abundance or biomass of invertebrate communities was analysed

by statistical program PRIMER (Clarke & Warwick, 2001). Non-metric multidimensional scaling analysis (MDS) of invertebrate abundance or biomass was used to quantify the dissimilarities between invertebrate communities. Bray-Curtis similarity measure was used to construct the similarity matrices (Bray & Curtis, 1957). A Spearman rank correlation ( $\rho$ ) was computed between the similarity matrices of invertebrate abundance or biomass and environmental data to examine the ecological significance of environmental variables on invertebrate assemblages (BIO-ENV procedure) and the significance of the correlation was determined by the PRIMER programme RELATE (Clarke & Ainsworth, 1993). The statistical differences in invertebrate assemblages between the predefined groups of samples were obtained by ANOSIM permutation test. The data was grouped as drift alga, sediment under algae, bare sediment and drift algae + sediment under algae. The contribution of different taxa in the differences was calculated by SIMPER procedure (Clarke, 1993). We employed linear and second-order polynomial linear regression analyses to describe the relationships between invertebrates and ambient environmental variables. Polynomial regression results are

only reported if significantly better fits were achieved using this method compared with the linear model.

## Results

The average total biomass of macrovegetation was  $347 \text{ g m}^{-2}$  ( $\pm \text{SE } 58$ ;  $N = 21$ ) in the presence of drift algae and only  $15 \text{ g m}^{-2}$  ( $\pm \text{SE } 9$ ;  $N = 15$ ) on adjacent bottoms. Algal biomass in the mat varied between 35 and  $1391 \text{ g dw m}^{-2}$ . The ephemeral brown algae *Pilayella littoralis* (L.) Kjellman prevailed both in algal mat and mat-free areas. Under the drift algae the reduced biomasses of attached *P. littoralis*, *Furcellaria lumbricalis* (Huds.) Lamouroux, *Polysiphonia nigrescens* (Huds.) Grev. and *Sphacellaria arctica* Harv. and a slight increase in the biomasses of *Potamogeton pectinatus* L., *P. perfoliatus* L. and *Zannichellia palustris* L. have been observed. *Chara* spp., *Tolypella nidifica* (Müller) Braun and *Cladophora glomerata* (L.) Kütz. were missing under the drift algae otherwise present on bare sediment (Table 1).

There was a significant difference in the abundance structure of infauna between bare sediment

Table 1. Mean biomasses ( $\text{g m}^{-2} \pm \text{SE}$ ) of phytobenthic species in different samples

Taxa	1	2	3
<i>Ceramium tenuicorne</i> (Kütz.) Waern	0	<0.01	0.18 $\pm$ 0.18
<i>Chara</i> spp.	0	0	0.02 $\pm$ 0.01
<i>Cladophora glomerata</i> (L.) Kütz.	6.77 $\pm$ 2.60	0	0.00
<i>Fucus vesiculosus</i> L.	2.17 $\pm$ 0.91	<0.01	0
<i>Furcellaria lumbricalis</i> (Huds.) Lamouroux	0.98 $\pm$ 0.40	0.00	0.28 $\pm$ 0.28
<i>Myriophyllum spicatum</i> L.	0.15 $\pm$ 0.08	0	0
<i>Phyllophora pseudoceranoides</i> S. G. Gmelin	0.01 $\pm$ 0.01	0	0
<i>Pilayella littoralis</i> (L.) Kjellm.	330.68 $\pm$ 78.88	3.65 $\pm$ 0.94	14.27 $\pm$ 5.04
<i>Polysiphonia nigrescens</i> (Huds.) Grev.	0.00	0	0.41 $\pm$ 0.41
<i>Potamogeton pectinatus</i> L.	0	<0.01	0
<i>Potamogeton perfoliatus</i> L.	<0.01	<0.01	0
<i>Rhodomela confervoides</i> (Huds.) Grev.	0.91 $\pm$ 0.51	0	0
<i>Ruppia maritima</i> L.	2.02 $\pm$ 1.14	0	0
<i>Sphacellaria arctica</i> Harv.	<0.01	<0.01	0.29 $\pm$ 0.29
<i>Stictyosiphon tortilis</i> (Rupr.) Reinke	<0.01	<0.01	<0.01
<i>Zannichellia palustris</i> L.	0.07 $\pm$ 0.04	<0.01	0
<i>Zostera marina</i> L.	<0.01	0	0
<i>Tolypella nidifica</i> (Müller) Braun	<0.01	0	0.03 $\pm$ 0.03

1 – Drift algae:  $N = 21$ ; 2 – Sediment under the drift algae  $N = 21$ ; 3 – Bare sediment:  $N = 15$ .

and sediment under the drift algae (ANOSIM,  $p = 0.006$ ) whereas the differences in the whole community structure (infauna + invertebrates associated with macroalgae) were not statistically significant (ANOSIM,  $p = 0.40$ ). On the other hand, the differences in the biomass structure of macrozoobenthos were statistically significant both for infauna (ANOSIM,  $p = 0.015$ ) and whole communities (ANOSIM,  $p = 0.002$ ). Sediment under the drift algae hosted less dense populations of *M. balthica*, *Hediste diversicolor* (Müller), *Hydrobia ulvae* (Pennant) and *Cerastoderma glaucum* (Bruguière) as compared to bare sediment. Under the drift algae the biomass of *M. balthica* was higher and the biomass of *Mya arenaria* L. and *C. glaucum* was lower as compared to bare sediment (Table 2).

When sediment and algal samples were pooled (infauna + invertebrates associated with macroalgae), the presence of drift algae coincided with the disappearance of *Oligochaeta* and *Lymnea* spp.

and appearance of *Prostoma obscurum* Schultze, *Saduria entomon* (L.), Chironomidae, *Gammarus oceanicus* Segerstråle, *Marenzelleria viridis* (Verrill) and *Idotea baltica* (Pallas), respectively. Increased abundance of *Hydrobia* spp. and biomass of *Hydrobia* spp. and *M. balthica* were observed at sites within the drift algae. The biomass of *C. glaucum* was reduced in the presence of the drift algae. Species composition was highly variable at sites affected by the drift algae indicated by lower within group similarities in SIMPER analysis.

Detritivores were the dominant functional group both within and outside the algal mat as infauna was included. In the drift algae herbivores were the most abundant group, while the biomasses of different functional groups in the drift algae were more evenly distributed. The abundance and biomass of herbivores and detritivores were higher in presence of the drift algae as compared to bare sediment communities. Mobile omni- and carnivorous species were positively influenced by the

Table 2. Mean abundances (ind m<sup>-2</sup> ± SE) and biomasses (g dw m<sup>-2</sup> ± SE) of zoobenthic taxa in different samples

Taxa	Abundance			Biomass		
	1	2	3	1	2	3
<i>Cerastoderma glaucum</i> (Bruguière)	17 ± 10	56 ± 18	96 ± 21	0.37 ± 0.21	0.70 ± 0.31	5.11 ± 1.37
Chironomidae	516 ± 272	1 ± 1	0	0.31 ± 0.16	<0.01	0
<i>Corophium volutator</i> (Pallas)	0	10 ± 6	7 ± 4	0	<0.01	<0.01
<i>Gammarus</i> juv.	45 ± 20	5 ± 3	8 ± 8	0.02 ± 0.01	<0.01	<0.01
<i>Gammarus oceanicus</i> Segerstråle	0	7 ± 3	0	0	<0.01	0
<i>Gammarus salinus</i> Spooner	47 ± 19	7 ± 3	2 ± 2	0.06	<0.01	<0.01
<i>Hediste diversicolor</i> (Müller)	67 ± 13	232 ± 49	341 ± 79	0.10 ± 0.04	1.00 ± 0.17	0.26 ± 0.05
<i>Hydrobia ulvae</i> (Pennant)	800 ± 292	137 ± 63	297 ± 60	1.92 ± 0.66	0.36 ± 0.17	1.01 ± 0.16
<i>Hydrobia ventrosa</i> (Montagu)	189 ± 65	7 ± 3	8 ± 4	0.20 ± 0.07	<0.01	0.01 ± 0.01
<i>Idotea baltica</i> (Pallas)	3 ± 2	0	0	0.05 ± 0.03	0	0
<i>Idotea chelipes</i> (Pallas)	8 ± 3	0	2 ± 2	<0.01	0	<0.01
<i>Jaera albifrons</i> Leach	11 ± 4	0	7 ± 7	<0.01	0	<0.01
<i>Lymnea</i> sp.	0	0	7 ± 4	0	0	0.26 ± 0.14
<i>Macoma balthica</i> (L.)	158 ± 52	727 ± 112	938 ± 135	10.55 ± 5.68	58.26 ± 9.20	51.92 ± 10.36
<i>Marenzelleria viridis</i> (Verrill)	0	7 ± 3	0	0	0.02 ± 0.01	0
<i>Mya arenaria</i> L.	10 ± 5	42 ± 7	72 ± 23	8.35 ± 4.66	6.67 ± 1.39	15.38 ± 5.43
<i>Mytilus edulis</i> L.	5 ± 3	20 ± 11	9 ± 4	0.16 ± 0.09	0.56 ± 0.31	0.09 ± 0.04
<i>Oligochaeta</i>	0	0	13 ± 7	0	0	<0.01
<i>Prostoma obscurum</i> Schultze	13 ± 7	0	0	<0.01	0	0
<i>Saduria entomon</i> (L.)	8 ± 3	5 ± 3	0	0.29 ± 0.15	0.02 ± 0.01	0
<i>Theodoxus fluviatilis</i> (L.)	73 ± 26	5 ± 3	23 ± 10	0.76 ± 0.36	0.07 ± 0.04	0.24 ± 0.09

1 – Drift algae ( $N = 21$ ), 2 – Sediment under the drift algae ( $N = 21$ ), 3 – Bare sediment ( $N = 15$ ).

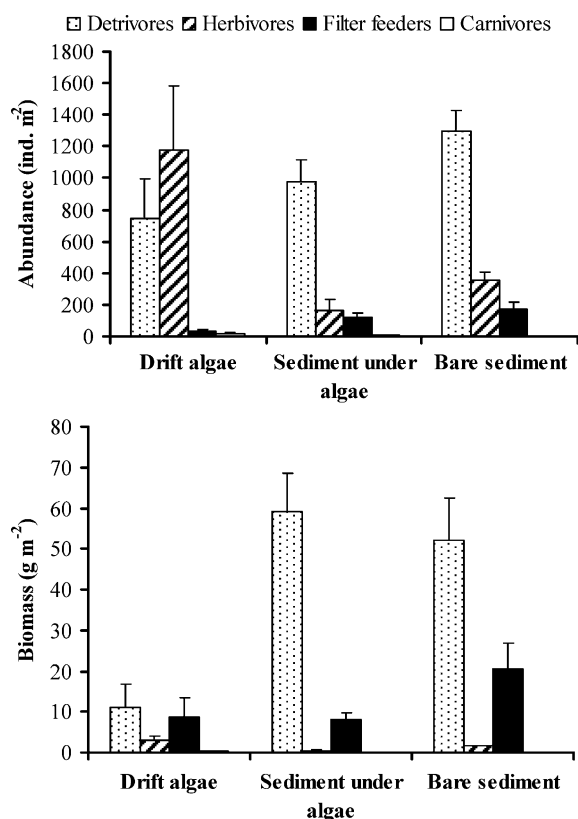


Figure 1. Mean ( $\pm$ S.E.) abundance (ind. m<sup>-2</sup>) and biomass values (g m<sup>-2</sup>) of invertebrate functional groups at different samples: drift algae ( $N = 21$ ), sediment under the drift algae ( $N = 21$ ) and bare sediment ( $N = 15$ ).

presence of drift algae as the predator *Saduria entomon* was found only within the drift algae (Fig. 1).

Among observed environmental parameters (oxygen concentration of nearbottom water, sediment type, thickness of algal mat and depth), the thickness of the mat and oxygen concentration gave the best match with the structure of zoobenthic communities (Table 3). Oxygen concentration at nearbottom layer decreased with increasing thickness of algal mat (linear regression analysis,  $r = 0.78$ ,  $p < 0.01$ ). The number of infaunal species did not change with the thickness of algal mat (linear regression analysis,  $p > 0.05$ ) whereas the total number of invertebrate species increased curvilinearly with the thickness of algal mat having the peak value at 3–5 cm thick algal mat (second-order polynomial regression analysis,  $r = 0.58$ ,  $p < 0.01$ ). The number of plant species

Table 3. Correlations (Spearman  $\rho$ ) between the structure of zoobenthic communities and the best-matching combinations of environmental parameters (oxygen concentration of the near-bottom water, sediment type, thickness of the algal mat, depth)

Model	Independent variables	$\rho$
<i>Drift algae</i>		
Abundance	Mat thickness	0.572
Biomass	Mat thickness	0.476
<i>Infauna (sediment under the drift algae and bare sediment)</i>		
Abundance	Oxygen concentration	0.226
Biomass	Oxygen concentration	0.270
<i>All communities</i>		
Abundance	Oxygen concentration, Mat thickness	0.414
Biomass	Oxygen concentration, Mat thickness	0.399

The significance of all correlations is less than 0.05.

increased with the thickness of algal mat (linear regression analysis,  $p < 0.001$ ,  $r = 0.87$ ). Total biomass of infauna and total biomass of all invertebrates did not change with the thickness of algal mat (linear regression analysis,  $p > 0.05$ ) (Fig. 2).

## Discussion

The present study showed that the thin drift algae had moderate effects on the structure of zoobenthic community. Although the thickness of algal cover was among the most important factors that affected zoobenthos, its influence appeared not to be degenerative except for a few infaunal species. The most destructive factor in connection with algal mats is hypoxia or anoxia in the bottom water and the sediment, often accompanied by the release of toxic hydrogen sulphide (Lavery & McComb, 1991; Krause-Jensen et al., 1999). Hypoxic conditions in nearbottom water are clearly shown to disturb benthic fauna, especially the groups with limited mobility (Everett, 1994; Norkko & Bonsdorff, 1996a). In addition, algal mats physically limit infauna to reach the normally oxygenated water layer (Norkko & Bonsdorff, 1996c). Similarly, in our study oxygen concentration of the bottom water was inversely related to the thickness of algal mats. The lower side of the

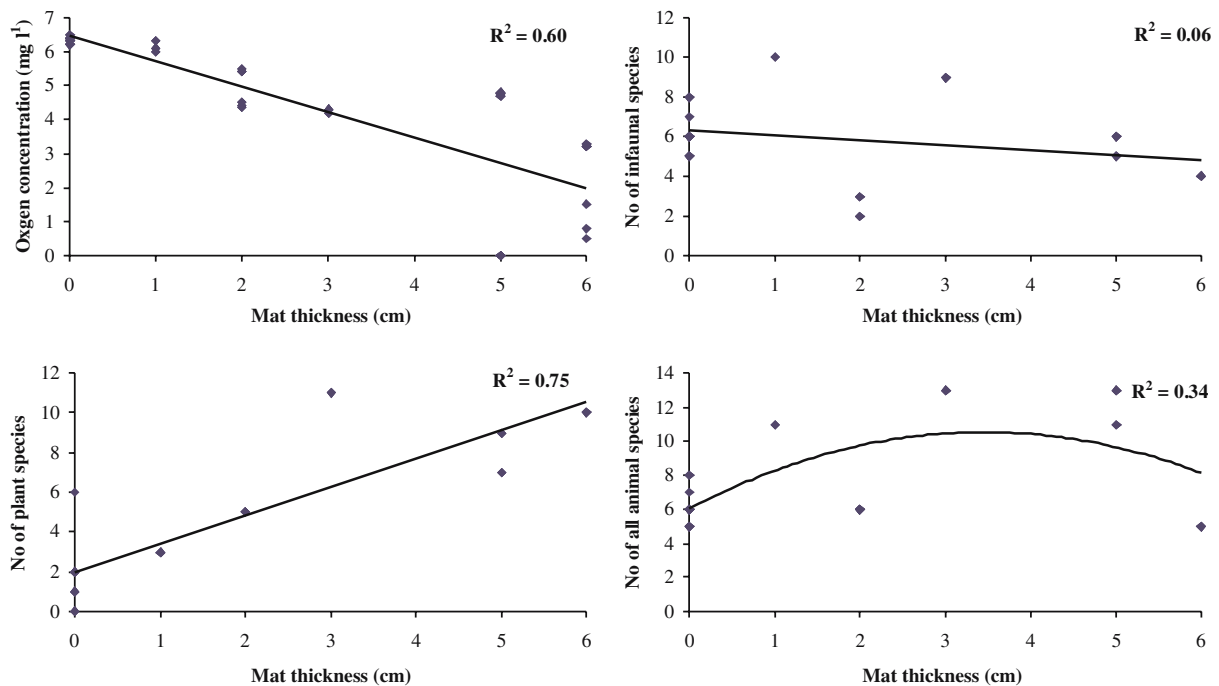


Figure 2. Relationships between the thickness of algal mat, benthic macrophytes and invertebrates.

thickest mat (6 cm) was black with strong odour indicating the recent formation of hydrogen sulphide. It is likely that in such a shallow area currents and waves are of great importance in sustaining normoxic conditions under the drift algal mats. Besides, occasional storm events prevent the development of very thick algal mats in our study area (Martin et al., 2003). In the Finnish coastal areas, the drift algal mats may occur in much deeper areas where anaerobic conditions are more likely to develop during the degradation process (Vahteri et al., 2000).

The impact of algal mats on zoobenthic communities depends on invertebrate species composition as different zoobenthic groups have shown dissimilar responses to the stress caused by algal mats (e.g. Everett, 1994). Intolerance towards algal mats is often connected to limited mobility, which disables rising to the upper layers of the mat in cases of oxygen deficiency (Norkko et al., 2000), but also to sensitivity to mechanical obstruction of feeding in some species (Everett, 1994; Raffaelli, 2000). The same species may react differently depending on environmental conditions. In this study we found no clear negative effects of algal mats on the prevailing clam species *M. balthica*

(i.e. increased biomasses and reduced abundances under the drift algae). The severe consequences of drift algal mats on the biomasses and recruitment of the clam *M. balthica* have been earlier reported (Ólafsson, 1988; Norkko & Bonsdorff, 1996b, c). However, the species has remained indifferent to algal mats in the studies conducted in other regions of the world (Everett, 1994; Thiel et al., 1998). Furthermore, the abundance of the clam may even increase under algal mat (Hull, 1987). One possible explanation is the lower tolerance of the species to complementary stress in the hypersaline conditions of the Baltic Sea. The key stress factor for the species may be the oxygen deficiency, as the species has been shown to be otherwise rather tolerant to organic loading and due to its feeding mode even be favoured by high organic inputs (Hull, 1987; Kotta & Kotta, 1995; Kotta, 2000). Nevertheless, even well-aerated algal mats may be destructive for the population of *M. balthica* in longer perspective by diminishing the recruitment success of the bivalve (Bonsdorff, 1992; Bonsdorff et al., 1995). Alternatively, predation of *S. entomon* on *M. balthica* (Sandberg, 1996) may explain the low number of the clams under the drift algae.

The polychaete *M. viridis* showed clear preference towards algal mats or higher content of organic matter under the mats. The gathering of the polychaetes under the algal mats has also been observed by other authors (Hull, 1987; Norkko & Bonsdorff, 1996a, b; Kotta & Orav, 2001) indicating their feeding on the decomposing algae (Raffaelli, 2000) and bioturbation induced facilitation of algal decomposition (Anderson & Meadows, 1978; Hansen & Kristensen, 1998). In addition to good feeding grounds, algal mats may also be beneficial for these polychaetes by offering shelter from predators, as is shown by Norkko (1997).

Mobile invertebrates should benefit from the drift algae due to the increased complexity of habitat (Paalme et al., 2002). However, common herbivorous and detritivorous arthropods of the study area poorly colonized the drift algae. A similar low preference of drift algae by herbivorous arthropods has been recorded earlier in the Baltic area (Norkko et al., 2000; Salovius & Bonsdorff, 2004) and may be explained by the species composition, as well as the degradation stage of the algal mats (Kotta et al., 2000; Orav-Kotta & Kotta, 2004).

The detritivore *Gammarus* spp. feed on more decomposed algae (Paalme et al., 2002) and it seems to be the case for Chironomidae larvae (Norkko et al., 2000) explaining their high densities among the drift algae. Among gastropods *T. fluviatilis*, although inhabiting the drift algae, showed moderate abundances as compared with *Hydrobia* spp. The fact, that *H. ulvae* prevailed in the drift algae, was rather predictable, as adult *Hydrobia* spp. have high migration rate towards additional food sources (Norkko & Bonsdorff, 1996b) while for juveniles selective settling on algal mats is shown (Cardoso et al., 2002). Thus, among a variety of herbivorous and detritivorous invertebrates practically only *Hydrobia* spp. potentially benefitted from the algal mats increasing their population densities and dispersing widely along the coastal sea.

Usually the overall effect of macroalgal blooms is the impoverishment of benthic communities. Stable long-lived oligotrophic communities, e.g. coral, seagrass and *Fucus vesiculosus* L. communities, are replaced by ephemeral seaweeds (Vogt & Schramm, 1991; Bell, 1992; Schramm,

1996; Valiela et al., 1997). As a consequence a habitat complexity and, thus, benthic biodiversity are likely to decrease. However, faunal diversity may increase under the algal cover in case the complexity of comparable undisturbed bottoms is naturally low (Everett, 1994).

Although the results of the present study show lack of strong negative effects of the thin algal mats on zoobenthos, the conclusions cannot be extended to a wider time- or depth-scale. The reaction of zoobenthos is likely to be year-dependant since the hydrodynamic conditions and the duration of the algal coverage vary between years. In the deeper sea the influence of algal accumulations on macrozoobenthos is severe as the algal mats are usually anoxic and the aeration by waves is much weaker than in shallower areas (Vahteri et al., 2000). Nevertheless, the present study assures that moderate algal mats at their peak occurrence have no impoverishing effect on the zoobenthic communities if water exchange is sufficient. Furthermore, algal mats attract various zoobenthic species and harbour remarkably more diverse macrofaunal communities in otherwise poorly vegetated coastal areas.

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