ORIGINAL ARTICLE

Effects of eelgrass *(Zostera marina)* canopy removal and sediment addition on sediment characteristics and benthic communities in the Northern Baltic Sea

Kristjan Herkül[1,2] & Jonne Kotta[1]

1 Estonian Marine Institute, University of Tartu, Tallinn, Estonia
2 Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

Abstract

The eelgrass *Zostera marina* is a key structural and functional species across the European coastline. The separate and interactive effects of eelgrass canopy removal and sediment addition on the sediment characteristics and the structure of benthic communities were studied in a factorial field experiment in the Northern Baltic Sea in July–August 2006. The removal of eelgrass canopy temporarily increased the sediment oxygen consumption, reduced the content of fine particles (<100 μm) and organic matter in the sediment, and increased the share of sand fraction (250–500 μm). Sediment addition increased the content of fine particles (<100 μm) and reduced the share of sand fraction (250–1000 μm). The effects were strongest in the presence of eelgrass canopy. Benthic invertebrates and macroalgae were affected by eelgrass canopy removal but not by sediment addition. The removal of eelgrass canopy significantly decreased benthic species richness and invertebrate and macroalgal densities. To conclude, our experiment demonstrates that *Z. marina* defines the patterns of benthic macroalgae and invertebrates but has moderate effects on sediment structure and metabolism in the Northern Baltic Sea.

Problem

Seagrasses have an important role in the coastal ecosystems worldwide. Seagrasses are known to stabilize the seabed in which they grow, reduce the resuspension of sediments, influence sediment deposition and composition (Terrados & Duarte 2000; Gacia *et al.* 2003; Bos *et al.* 2007; Hasegawa *et al.* 2008; Hendriks *et al.* 2008), release oxygen into the sediment (Enríquez *et al.* 2001; Frederiksen & Glud 2006), and provide habitat and food for a great variety of plant and animal species (Rasmussen 1973; Orth *et al.* 1984; Orth 1992; Mattila *et al.* 1999; Heck *et al.* 2003).

The eelgrass *Zostera marina* is a key structural and functional species across the European coastline. *Zostera marina* grows on a wide range of soft and mixed sediments, and their roots are, in many cases, growing in anoxic environments. To maintain oxygen in their root systems, seagrasses have adapted an O_2 transport system

from leaves to roots (Pedersen *et al.* 1998; Frederiksen & Glud 2006). Oxygen loss from the roots into the sediment may occur, providing an oxidative protection against phytotoxins such as Fe^{2+}, Mn^{2+} and sulfides (Penhale & Wetzel 1983; Frederiksen & Glud 2006). The release of oxygen by the roots may indirectly accelerate the decomposition of sediment organic matter and facilitate the development of benthic infauna. On the other hand, seagrasses may increase the content of organic matter and fine particles in sediment by increasing sedimentation through a reduction of current velocity (Fonseca & Fisher 1986), direct trapping and binding of particles (Hendriks *et al.* 2008) and enhancing sediment accretion (Bos *et al.* 2007). Lower current velocity also leads to increased settlement of macroalgae, pelagic larvae and juveniles of benthic invertebrates and thus fosters the diversity and density of plant and animal species within the seagrass canopy (Reusch 1998; Bologna *et al.* 2005).

In recent decades the abundance and spatial extent of seagrasses around the world has been declining and this loss has been mainly associated to elevated anthropogenic eutrophication and intensified sediment dynamics (Duarte 2002; Orth *et al.* 2006; Cabaco *et al.* 2008b). Anthropogenic eutrophication is known to reduce light levels for seagrasses, leading to the removal of the seagrass canopy (Short *et al.* 1995; Longstaff *et al.* 1999; Duarte 2002; Hauxwell *et al.* 2003; Cardoso *et al.* 2004; Cabaço *et al.* 2008a). Similar effects have been observed with increasing grazing pressures (Wressnig & Booth 2008). Recent shifts in climate conditions have resulted in elevated winter temperatures and reduced extent and duration of ice cover in Northern Europe (Jaagus 2006). Due to the continuous decrease of the ice cover the winter storms are likely to have increasing ecological impacts on shallow water seagrass communities. Such storms involve frequent burial of seagrasses under sediment and/or removal of the seagrass canopy. As a consequence of canopy disappearance the important functions provided by seagrasses are likely lost in coastal ecosystems.

There are many observational studies comparing benthic communities among vegetated and unvegetated seagrass habitats (*e.g.* Boström & Bonsdorff 1997; Turner *et al.* 1999; Nagelkerken & van der Velde 2004; Nakamura & Sano 2005). Without experimenting, however, these studies are unable to distinguish the effects of seagrasses and provide circumstantial evidence on the difference between vegetated and unvegetated habitats. In fact, these differences can be due to factors other than seagrasses. There exist a few experimental studies that describe the structure of seagrass communities but there are virtually no experimental studies that measure a function in relation to the characteristics of seagrass habitat (Davis & Fourqurean 2001; Pereg-Gerk *et al.* 2002). To date the manipulative studies on seagrasses have been carried out in subtropical or tropical ecosystems, but not in temperate ecosystems.

In this study we experimentally evaluated the separate and interactive effects of *Z. marina* canopy removal and sand addition on sediment characteristics and structure of benthic communities. Our hypotheses were as follows: (i) eelgrass decreases oxygen flux through the sediment–water interface, (ii) eelgrass increases the content of organic matter and fine particles in sediment, (iii) removal of eelgrass reduces benthic biodiversity and (iv) sand addition weakens the effects of eelgrass.

Material and Methods

Study area

Experiments were performed near Prangli Island (59.610°N, 25.004°E), Gulf of Finland, Northern Baltic Sea. The average salinity in the area is 6 psu. Sand and gravel dominate, but stand-alone stones are also found in shallow waters. As the Baltic Sea is a nontidal system, the experimental area is constantly submerged and strongly influenced by currents and wave action. The study area has naturally very sorted sediments, *i.e.* medium to coarse sand with very low content of fine sediment fractions and organic matter. The average biomass of the above-ground parts of *Zostera marina* in the experimental area was 58.0 ± 11.2 g dw m^{-2}.

Experimental design

The *in situ* factorial field experiment was carried out from 2 July until 28 August 2006. The 50×50 cm experimental plots were placed in a natural *Z. marina* bed at 4 m depth. The experimental design included two manipulative treatments: canopy removal and sediment addition. The canopy removal treatment had two levels: presence and absence of eelgrass canopy. The treatment without eelgrass canopy was established by manually removing all above-ground parts of eelgrass prior to experiment. Additionally, new shoots were systematically removed in each sampling occasion. We did not attempt to remove roots as this would disrupt too much sediment structure and associated infauna and would not happen in nature. The disappearance of canopy, however, is a very likely event at elevated eutrophication (low light levels) and/or grazing pressure. The treatment of sediment addition also had two levels: sediment was either added or not added. The treatment was established by adding a 2-cm layer of natural seabed sediment to the experimental plots. Prior to the experiment the sediment was sun-dried for several days to ensure that it was free of living benthic invertebrates. It was also visually checked that the sediment was devoid of living animals. This 2×2 factorial design was replicated three times, resulting in a total of 12 experimental plots.

Sampling and processing

Oxygen flux through sediment–water interface, sediment granulometry and sediment organic matter content was measured four times: immediately after setting up the experimental plots on 2 July and then on 15 July, and 7 and 28 August. Samples for benthic invertebrates and macrophytes were collected only at the end of the experiment (*i.e.* on 28 August). Transparent acrylic cores (3.6 cm inner diameter, 27 cm length) with rubber stoppers for both ends were used to measure oxygen flux and to sample sediment for granulometric and organic content analyses. Oxygen flux through the sediment–water interface was studied in light. The cores were inserted

into sediment to a depth of 10 cm and the upper ends of the cores were closed with rubber stoppers. As seagrass cover was always below 100% we could avoid plant leaves in the cores. Thus, the design allowed a direct comparison of oxygen flux between treatments without having to correct for the relative amount of seagrass leaves. One core was inserted into each experimental plot. Oxygen concentrations in the cores were measured polarographically before and after a 2.5-h incubation using a WTW OXI 92 oxygen meter. The cores were taken out from the sediment after incubation, retaining the sediment inside the core for further analyses of the content of organic matter and sediment granulometry. The sediment samples were packed into plastic jars and kept in deep freezer (−18 °C). In the laboratory the sediment samples were melted, homogenized and subsamples for the analyses of organic matter content and granulometry were taken from each sample. The organic matter content was measured as a percentage loss of weight on ignition (500 °C, 3 h) of dry sediment (60 °C, 7 days). For granulometric analysis, dry sediment (60 °C, 7 days) was sieved through a set of sieves of decreasing mesh size (2000, 1000, 500, 250, 100, 63 μm) stacked vertically and placed in a vibratory sieve shaker. The sediment retained in each sieve and the sediment penetrating the 63-μm sieve were weighed (precision of 0.001 g). A core of 10.3 cm diameter was used for macrobenthos sampling. One sample was taken from each plot. Benthos samples were sieved in the field on 0.25-mm mesh screens. The samples were stored in a deep freezer (−18 °C). In each sample, all macroscopic plants and animals were picked out and identified to the species level except for juvenile gammarid amphipods, chironomid larvae and oligochaetes. Dry biomass (60 °C for 2 weeks) of each plant taxon and dry biomass and abundance of each animal taxon were estimated (precision of 0.0001 g).

Statistical methods

Two-way factorial ANOVA (StatSoft Inc. 2007) with canopy removal and sediment addition as factors was used to assess differences in oxygen flux, organic matter content of sediment, total abundance, biomass and species richness of macrobenthos separately by each sampling date. Pooled data of sediment granulometry (mass percentage of each grain size group) from sampling dates 2–4 were analysed using two-way factorial ANOVA with the eelgrass canopy removal and sediment addition as factors. PERMANOVA (Anderson *et al.* 2008) was used to test for differences in the abundance and biomass structure of benthic invertebrates and in the biomass structure of benthic macrophytes among the studied treatments. Data was fourth root-transformed prior to running PERMANOVA

to down weight the dominant species and increase the contribution of rarer species in the multivariate analysis (Anderson *et al.* 2008). Non-metric multidimensional scaling (MDS; Clarke & Warwick 2001) on fourth root-transformed data was used to visualize differences in the structure of benthos.

Results

Sediment characteristics

Oxygen measurements showed that all incubated sediments consumed oxygen (Table 1). The oxygen consumption varied between 28 and 198 mg m^{-2} h^{-1} with an average of 87 mg m^{-2} h^{-1}. The plots without eelgrass canopy consumed significantly more oxygen (81 mg m^{-2} h^{-1}) than those with eelgrass canopy (51 mg m^{-2} h^{-1}) but significant differences were observed only in the third sampling (Tables 1 and 2). The effects of sediment addition and interaction between canopy removal and sediment addition were not statistically significant (Table 2).

Similarly to the oxygen flux, the content of organic matter in sediment significantly differed between plots with eelgrass canopy (0.57%) and without eelgrass canopy (0.46%) on the third sampling occasion. No other significant differences were found (Table 3).

As compared to the plots without eelgrass canopy, the plots with eelgrass canopy were characterized by a significantly higher proportion of fine particles (<63 μm: 1.29% *versus* 1.80%; 63–100 μm: 11.64% *versus* 14.15%) and lower proportion of sand fraction (250–500 μm: 9.07% *versus* 7.05%) (Table 4). The proportion of fine particles (<100 μm) was higher on the plots with added sediment (15.10%) than on the control plots (13.77%). The share of sand fraction (250–1000 μm) was lower on the plots with added sediment (11.73%) than on the control plots (13.83%). These effects were strongest in the presence of eelgrass canopy.

Benthic community

A total of 17 invertebrate taxa and seven macrophyte species were identified in benthos samples. PERMANOVA tests revealed that there were significant differences in the abundance and biomass structure of zoobenthos and biomass structure of phytobenthos between plots with and without eelgrass canopy (Table 5, Fig. 1). Sediment addition and the interactive effects of canopy removal and sediment addition were not statistically significant. The plots with removed canopy were mainly characterized by a significantly lower density of *Gammarus* spp., *Idotea balthica*, *Corophium volutator*, and *Hydrobia ulvae* (see

Table 1. Mean values and standard errors (SE) on oxygen flux through sediment–water interface, content of organic matter in sediment and sediment grain size at different treatment levels.

Date	Treatment Canopy	Treatment Sediment	Oxygen flux (mg m^{-2} h^{-1} ± SE)	Organic content (% ± SE)	Sediment grain size (% ± SE) <63 µm	63–100 µm	100–250 µm	250–500 µm	500–1000 µm	1000–2000 µm	>2000 µm
07/02	removed	not added	83.1 ± 29.4	0.63 ± 0.03	1.29 ± 0.09	12.88 ± 0.75	59.13 ± 1.96	9.58 ± 0.65	4.52 ± 0.25	2.85 ± 0.05	9.74 ± 2.57
07/02	removed	added	137.7 ± 14.3	0.6 ± 0.05	1.44 ± 0.14	12.69 ± 1.21	52.53 ± 0.67	8.16 ± 0.58	4.62 ± 0.34	3.13 ± 0.23	17.43 ± 0.72
07/02	not removed	not added	123.7 ± 38.8	0.54 ± 0.01	1.25 ± 0.29	11.64 ± 0.56	49.86 ± 0.73	9.03 ± 0.49	6.24 ± 0.74	3.27 ± 0.22	18.71 ± 2.18
07/02	not removed	added	111.7 ± 23.1	0.72 ± 0.08	1.73 ± 0.14	12.94 ± 1.28	49.25 ± 3.67	6.73 ± 0.95	4.37 ± 0.36	2.88 ± 0.3	22.1 ± 5.73
07/15	removed	not added	94.3 ± 8.2	0.6 ± 0.04	1.26 ± 0.09	11.99 ± 0.7	55.12 ± 1.6	10.38 ± 0.23	5.28 ± 0.11	2.72 ± 0.33	13.26 ± 2
07/15	removed	added	86.7 ± 25.3	0.59 ± 0.14	1.31 ± 0.25	11.62 ± 2.12	48.48 ± 5.53	8.03 ± 0.55	4.58 ± 0.35	2.87 ± 0.48	23.11 ± 8.11
07/15	not removed	not added	102.2 ± 8	0.6 ± 0.02	1.64 ± 0.28	13.33 ± 0.36	52.86 ± 1.39	8.33 ± 1.07	5.44 ± 0.59	3.49 ± 0.46	14.92 ± 1.54
07/15	not removed	added	51.4 ± 15.8	0.58 ± 0.03	1.81 ± 0.12	13.23 ± 0.64	50.61 ± 2.42	6.32 ± 0.37	4.04 ± 0.51	3 ± 0.65	20.99 ± 4.49
08/07	removed	not added	94.1 ± 20.1	0.43 ± 0.02	1.21 ± 0.06	11.69 ± 0.58	50.17 ± 3.53	8.51 ± 0.8	3.95 ± 0.35	2.4 ± 0.47	22.07 ± 5.24
08/07	removed	added	68.3 ± 7.9	0.49 ± 0.06	1.3 ± 0.15	11.44 ± 1.06	49.22 ± 4.18	8.81 ± 0.57	5.1 ± 0.36	3.88 ± 0.98	20.24 ± 4.53
08/07	not removed	not added	50.4 ± 8.2	0.55 ± 0.06	1.73 ± 0.22	13.91 ± 0.73	54.63 ± 1.48	8.84 ± 0.5	5.8 ± 0.82	3.37 ± 0.55	11.72 ± 3.55
08/07	not removed	added	51.6 ± 1.6	0.6 ± 0.04	1.89 ± 0.04	15.14 ± 0.4	53.54 ± 2.4	5.39 ± 0.28	3.13 ± 0.16	2.12 ± 0.09	18.8 ± 2.45
08/28	removed	not added	74.2 ± 9.4	0.47 ± 0.03	1.17 ± 0.1	10.75 ± 0.71	52.26 ± 2	9.08 ± 1.06	5.21 ± 1.08	3.26 ± 0.37	18.27 ± 1.2
08/28	removed	added	53.6 ± 5.7	0.85 ± 0.42	1.46 ± 0.04	12.35 ± 0.38	50.93 ± 3.01	9.59 ± 0.75	5.71 ± 0.4	3.37 ± 0.38	16.6 ± 3.47
08/28	not removed	not added	86.8 ± 27.1	0.57 ± 0.1	1.64 ± 0.12	13.04 ± 0.54	52.14 ± 2.37	7.96 ± 0.5	5.06 ± 1.15	3.42 ± 0.52	16.74 ± 0.87
08/28	not removed	added	105.1 ± 27.3	0.61 ± 0.01	2.1 ± 0.1	16.25 ± 1.03	55.36 ± 4.37	5.48 ± 0.34	3.36 ± 0.21	2.17 ± 0.04	15.28 ± 5.07

Table 2. Two-way ANOVA of sediment oxygen flux by each sampling date. Significant P-values are indicated in bold.

Date	Canopy removal		Sediment addition		Canopy × Sediment	
	F	P	F	P	F	P
2/7/2006	0.0686	0.8000	0.5839	0.4667	1.4280	0.2663
15/7/2006	0.7226	0.4200	2.3751	0.1618	2.6152	0.1445
7/8/2006	6.8324	**0.0309**	1.1309	0.3186	1.3623	0.2768
28/8/2006	2.5713	0.1475	0.0034	0.9549	0.9515	0.3579

Table 3. Two-way ANOVA of sediment organic matter content by each sampling date. Significant P-values are indicated in bold.

Date	Canopy removal		Sediment addition		Canopy × Sediment	
	F	P	F	P	F	P
2/7/2006	0.1132	0.7452	2.4684	0.1548	4.7696	0.0605
15/7/2006	0.0032	0.9559	0.3158	0.5895	0.7834	0.4019
7/8/2006	5.5276	**0.0466**	1.4174	0.2680	0.0337	0.8590
28/8/2006	0.1115	0.7470	0.9956	0.3476	0.6194	0.4540

Table 4. Two-way ANOVA of sediment grain size groups (mass percentage data) from sampling dates 2–4. Significant P-values are indicated in bold.
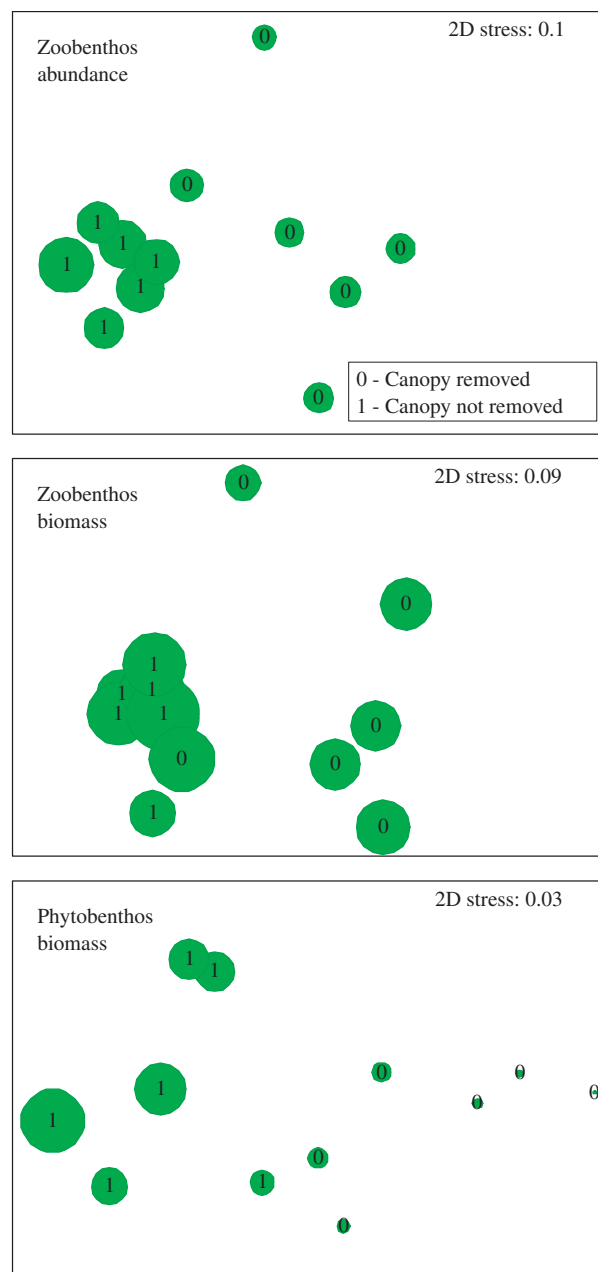
Grain size	Canopy removal		Sediment addition		Canopy × Sediment	
	F	P	F	P	F	P
<63 μm	41.0441	**<0.0001**	7.3704	**0.0106**	0.3673	0.5487
63–100 μm	24.2301	**<0.0001**	4.7397	**0.0370**	0.4376	0.5130
100–250 μm	1.6209	0.2121	0.0422	0.8386	0.0332	0.8566
250–500 μm	27.1953	**<0.0001**	11.0409	**0.0022**	12.5157	**0.0013**
500–1000 μm	2.1394	0.1533	5.7887	**0.0221**	10.2794	**0.0030**
1000–2000 μm	0.2830	0.5984	1.8631	0.1818	4.5245	**0.0412**
>2000 μm	1.2335	0.2750	0.4481	0.5080	1.1002	0.3021

Table 5. PERMANOVA of benthic community structure at the end of the experiment. Significant P-values are indicated in bold.

	Canopy removal		Sediment addition		Canopy × Sediment	
	F	P	F	P	F	P
Zoobenthos abundance	6.5193	**0.0026**	0.7209	0.5350	1.3926	0.2763
Zoobenthos biomass	4.7689	**0.0137**	0.8505	0.4669	1.3710	0.2753
Phytobenthos biomass	12.3710	**0.0016**	0.6548	0.5733	1.2348	0.3113

Fig. 1. MDS ordination of zoobenthos abundance and biomass structure and phytobenthos biomass structure. The number shows the factor level and the relative size of the bubbles indicates the total abundance or biomass of benthic organisms in a sample.

Z. marina) (Table 6). The sediment addition did not significantly affect the biomass of *Z. marina*.

Discussion

In this study we showed that (i) eelgrass canopy had moderate effects on sediment structure and metabolism, and (ii) benthic invertebrates and macroalgae were
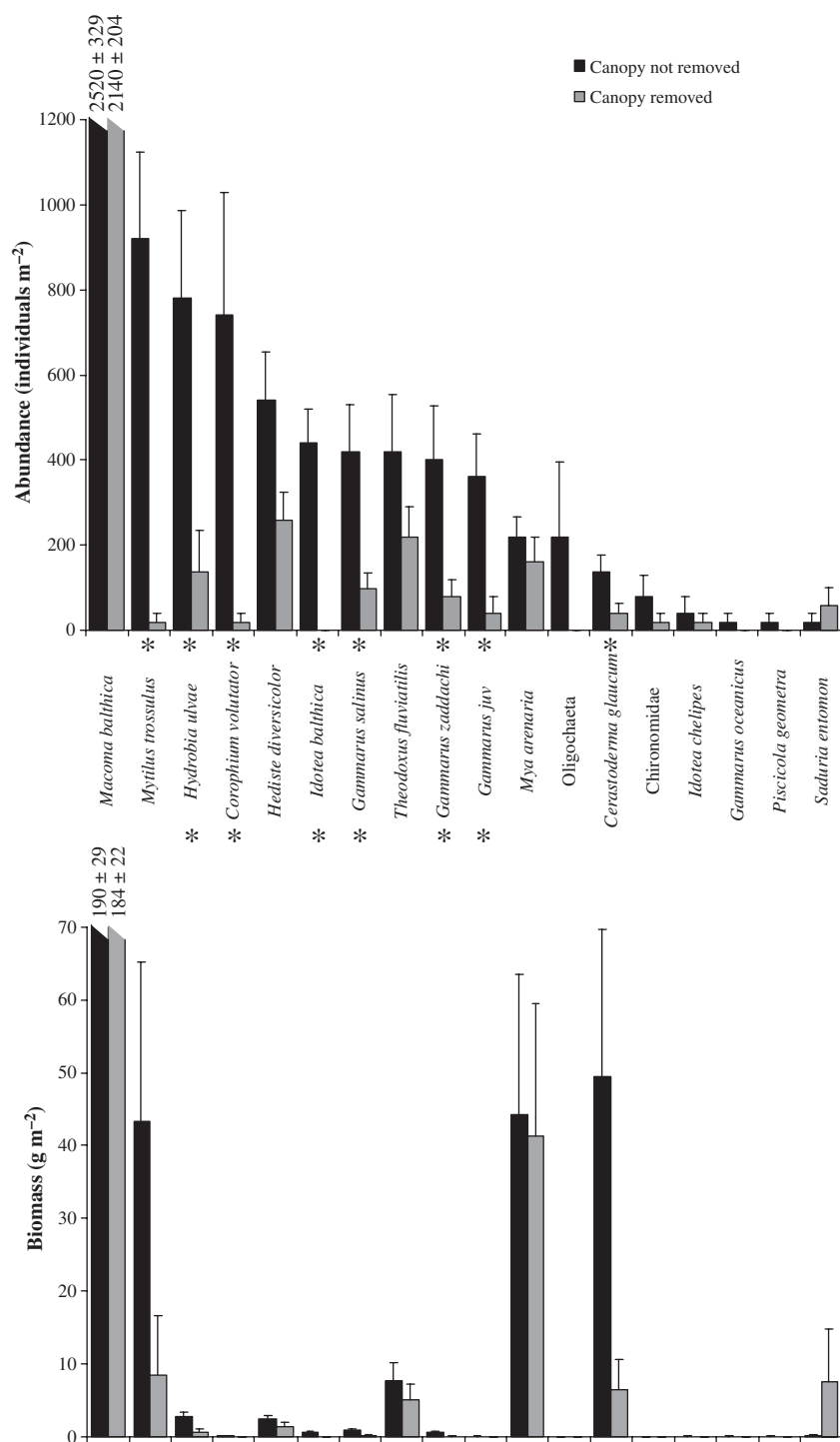
Fig. 2 for details). The removal of eelgrass decreased the biomass of all phytobenthic species but none of these differences was statistically significant.

Removal of the canopy significantly decreased the total abundance and species number of zoobenthos and total biomass and species richness of phytobenthos (excluding

Fig. 2. Macrozoobenthic community abundances (number of individuals m^{-2} ± SE; upper graph) and biomasses (g m^{-2} ± SE; lower graph) of the experimental plots with the canopy of *Zostera marina* removed and the canopy of *Zostera marina* not removed. Asterisk denotes significant differences in ANOVA analyses (P < 0.05).

affected by eelgrass canopy removal but not by sediment addition. *Zostera marina* decreased the oxygen flux through the sediment–water interface on the third sam-

pling. During the third sampling higher seawater temperatures were measured compared to other sampling periods and this may explain the significant differences in

Table 6. Two-way ANOVA of benthic community characteristics at the end of the experiment. Significant P-values are shown in bold.

	Canopy removal		Sediment addition		Canopy × Sediment	
	F	P	F	P	F	P
Total abundance of zoobenthos	30.3035	**0.0006**	0.2586	0.6248	0.4697	0.5125
Total biomass of zoobenthos	2.7208	0.1377	1.5953	0.2421	2.8320	0.1309
Number of zoobenthos species	29.4694	**0.0006**	0.0816	0.7824	0.3265	0.5834
Total biomass of phytobenthos	12.3267	**0.0080**	0.7171	0.4217	0.9384	0.3611
Number of phytobenthos species	9.0000	**0.0171**	0.0000	1.0000	0.0000	1.0000

oxygen demand. The relatively low contribution of eelgrass to the oxygen flux agrees with previous results of Pedersen *et al.* (1998) and Frederiksen & Glud (2006) who found that *Cymodocea rotundata* contributed only 1% and *Z. marina* 12% of the total oxygen flux.

Similarly to the oxygen flux, eelgrass canopy had a moderate effect on the content of organic matter in sediment. The content of organic matter was higher on plots with eelgrass canopy compared to plots where the canopy was removed. A similar facilitative effect of seagrass on sedimentation was documented for different seagrass species (Agawin & Duarte 2002; Peterson *et al.* 2004; Hendriks *et al.* 2008). We also found that eelgrass significantly increased the sedimentation of fine particles (grain size <100 *μ*m). This result was in accordance with the findings of an intertidal *Z. marina* bed (Bos *et al.* 2007), highlighting the role of eelgrass in the increase of water transparency by trapping fine suspended material.

In our study both univariate and multivariate community measures showed that the eelgrass canopy significantly promoted diversity and increased density of benthic macroalgae and invertebrates. Such a facilitating effect has been reported earlier for seagrass species in the Baltic Sea and elsewhere (Reusch & Chapman 1995; Boström & Bonsdorff 1997, 2000; Turner *et al.* 1999; Alfaro 2006). The losses due to the removal of eelgrass canopy can be attributed to the loss of habitat complexity and food. Eelgrass is known to be an important substratum for filamentous algae on soft sediments (Borum 1985) and the removal of eelgrass canopy reduces the biomass of macroalgae and, consequently, causes the decrease in the density of herbivores such as gammarid amphipods and *Idotea balthica*. The removal of eelgrass canopy significantly decreased the abundance of *Mytilus trossulus* in our study. *Zostera marina* is known to facilitate the settle-

ment of mussel larvae and also to provide a more stable habitat for adults (Reusch & Chapman 1995; Bologna *et al.* 2005). The removal of eelgrass canopy also decreased the densities of infaunal deposit feeders *Hediste diversicolor* and *Corophium volutator*, which can be attributed to the lower sedimentation rate of suspended matter and algal debris.

Sand addition had moderate effects on the sediment granulometry but no effects on oxygen flux through sediment–water interface and seagrass community structure. Similarly, no consistent interactive effects between seagrass canopy removal and sediment addition were found. The lack of significant effects might be attributed to naturally strong wave disturbance in our study area, *i.e.* the seagrass community is likely adapted to high sediment mobility.

To conclude, our experiment demonstrates that *Z. marina* defines the patterns of benthic macroalgae and invertebrates but has moderate effects on sediment granulometry, organic matter content and oxygen flux through the sediment–water interface. However, intensified sediment dynamics such as the burial of seagrasses under sand has no clear effects on the structure and functioning of seagrass communities in the Northern Baltic Sea. The results are also in agreement with earlier observational studies that compared the structure of benthic communities in vegetated and unvegetated seagrass habitats. All this suggests that *Z. marina* may survive moderate physical disturbances and counteract the effect of eutrophication by increasing sedimentation of fine particles, adding oxygen to the sediment, and providing habitat for many infaunal and epifaunal species.

Acknowledgements

References

Agawin N.S.R., Duarte C.M. (2002) Evidence of direct particle trapping by a tropical seagrass meadow. *Estuaries*, **25**, 1205–1209.

Alfaro A.C. (2006) Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuarine, Coastal and Shelf Science*, **66**, 97–110.

Anderson M.J., Gorley R.N., Clarke K.R. (2008) *PERMANO-VA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, UK.

Bologna P.A.X., Fetzer M.L., McDonnell S., Moody E.M. (2005) Assessing the potential benthic-pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. *Journal of Experimental Marine Biology and Ecology*, **316**, 117–131.

Borum J. (1985) Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology*, **87**, 211–218.

Bos A.R., Bouma T.J., de Kort G.L.J., van Katwijk M.M. (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuarine, Coastal and Shelf Science*, **74**, 344–348.

Boström C., Bonsdorff E. (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research*, **37**, 153–166.

Boström C., Bonsdorff E. (2000) Zoobenthic community establishment and habitat complexity – the importance of seagrass shoot density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series*, **205**, 123–138.

Cabaço S., Machás R., Vieira V., Santos R. (2008a) Impacts of urban wastewater discharge on seagrass meadows (*Zostera noltii*). *Estuarine, Coastal and Shelf Science*, **78**, 1–13.

Cabaço S., Santos R., Duarte C.M. (2008b) The impact of sediment burial and erosion on seagrasses: a review. *Estuarine, Coastal and Shelf Science*, **79**, 354–366.

Cardoso P.G., Pardal M.A., Lillebø A.I., Ferreira S.M. (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology*, **302**, 233–248.

Clarke K.R., Warwick R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth, UK.

Davis B.C., Fourqurean J.W. (2001) Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany*, **71**, 217–232.

Duarte C.M. (2002) The future of seagrass meadows. *Environmental Conservation*, **29**, 192–206.

Enríquez S., Marbà N., Duarte C.M., van Tussenbroek B.I., Reyes-Zavala G. (2001) Effects of seagrass *Thalassia testudinum* on sediment redox. *Marine Ecology Progress Series*, **219**, 149–158.

Fonseca M.S., Fisher J.S. (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series*, **29**, 15–22.

Frederiksen M.S., Glud R.N. (2006) Oxygen dynamics in the rhizosphere of *Zostera marina*: a two-dimensional planar optode study. *Limnology and Oceanography*, **51**, 1072–1083.

Gacia E., Duarte C.M., Marba N., Terrados J., Kennedy H., Fortes M.D., Huang N. (2003) Sediment deposition and production in SE Asia seagrass meadows. *Estuarine, Coastal and Shelf Science*, **56**, 909–919.

Hasegawa N., Hori M., Mukai H. (2008) Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment-water column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia*, **596**, 387–399.

Hauxwell J., Cebrián J., Valiela I. (2003) Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series*, **247**, 59–73.

Heck K.L. Jr, Hays G., Orth R.J. (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, **253**, 123–136.

Hendriks I.E., Sintes T., Bouma T.J., Duarte C.M. (2008) Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Marine Ecology Progress Series*, **356**, 163–173.

Jaagus J. (2006) Trends in sea ice conditions in the Baltic Sea near the Estonian coast during the period 1949/1950–2003/2004 and their relationships to large-scale atmospheric circulation. *Boreal Environment Research*, **11**, 169–183.

Longstaff B.J., Loneragan N.R., O'Donohue M.J., Dennison W.C. (1999) Effects of light deprivation on the survival and recovery of the seagrass *Halophila ovalis* (R.Br.) Hook. *Journal of Experimental Marine Biology and Ecology*, **234**, 1–27.

Mattila J., Chaplin G., Eilers M.R., Heck K.L., O'Neal J.P., Valentine J.F. (1999) Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research*, **41**, 321–332.

Nagelkerken I., van der Velde G. (2004) A comparison of fish communities of subtidal seagrass beds and sandy seabeds in 13 marine embayments of a Caribbean island, based on species, families, size distribution and functional groups. *Journal of Sea Research*, **52**, 127–147.

Nakamura Y., Sano M. (2005) Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. *Fisheries Science*, **71**, 534–550.

Orth R.J. (1992) A perspective on plant–animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John D.M., Hawkins S.J., Price J.H. (Eds), *Plant–Animal Interactions in the Marine Benthos*. Systematics Association Special Vol. 46, Clarendon Press, Oxford: 147–164.

Orth R.J., Heck K.L. Jr, van Montfrans J. (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries*, **7**, 339–350.

Orth R.J., Carruthers T.J.B., Dennison W.C., Duarte C.M., Fourqurean J.W., Heck K.L. Jr, Hughes A.R., Kendrick G.A., Kenworthy W.J., Olyarnik S., Short F.T., Waycott M., Williams S.L. (2006) A global crisis for seagrass ecosystems. *BioScience*, **56**, 987–996.

Pedersen O., Borum J., Duarte C.M., Fortes M.D. (1998) Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. *Marine Ecology Progress Series*, **169**, 283–288.

Penhale P.A., Wetzel R.G. (1983) Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. *Canadian Journal of Botany*, **61**, 1421–1428.

Pereg-Gerk L., Sar N., Lipkin Y. (2002) In situ nitrogen fixation associated with seagrasses in the Gulf of Elat (Red Sea). *Aquatic Ecology*, **36**, 387–394.

Peterson C.H., Luettich R.A. Jr, Micheli F. (2004) Attenuation of water flow inside seagrass canopies of differing structure. *Marine Ecology Progress Series*, **268**, 81–92.

Rasmussen E. (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia*, **11**, 1–495.

Reusch T.B.H. (1998) Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. *Marine Ecology Progress Series*, **167**, 149–153.

Reusch T.B.H., Chapman A.R.O. (1995) Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.)

beds. *Journal of Experimental Marine Biology and Ecology*, **192**, 257–271.

Short F.T., Burdick D.M., Kaldy J.E. III (1995) Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography*, **40**, 740–749.

StatSoft Inc. (2007) *Electronic Statistics Textbook*. StatSoft, Tulsa, OK. Available at: http://www.statsoft.com/textbook/stathome.html (last accessed on 11 June 2009).

Terrados J., Duarte C.M. (2000) Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. *Journal of Experimental Marine Biology and Ecology*, **243**, 45–53.

Turner S.J., Hewitt J.E., Wilkinson M.R., Morrisey D.J., Thrush S.F., Cummings V.J., Funnell G. (1999) Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries*, **22**, 1016–1032.

Wressnig A., Booth D.J. (2008) Patterns of seagrass biomass removal by two temperate Australian fishes (Monacanthidae). *Marine and Freshwater Research*, **59**, 408–417.