Effect of physical disturbance on the soft sediment benthic macrophyte and invertebrate community in the northern Baltic Sea

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Strong storms and ice scour are the most severe physical disturbances in the shallow water areas of the northern Baltic Sea. We studied experimentally the effects a physical disturbance — such as the removal of the surface sediment layer, vegetation, and benthic invertebrates and the timing of this disturbance (spring, summer) — had on the development of soft bottom macrophyte and invertebrate communities in a shallow bay. Disturbance had an immediate effect on the community in spring but not in summer. The lack of significant immediate effects in summer was attributed to a drifting algal mat that quickly introduced most of the local species to the newly established experimental plots. The springtime disturbance reduced the species richness and total biomass of phytobenthos in summer; the effect, however, was not detectable by autumn. Disturbance in spring decreased the total abundance and biomass of zoobenthos in autumn but not in summer. A summertime disturbance had no effect on the autumn benthic communities.

Introduction

Disturbance is a key factor regulating the structure and functioning of natural communities (Sousa 1984, Whitlatch *et al.* 1998, Zajac *et al.* 1998, Widdicombe and Austen 2001, Dernie *et al.* 2003). Numerous studies on physical disturbances in marine environments focused either on intertidal systems (e.g. Kim and DeWreede 1996, Hall and Harding 1997, Keough and Quinn 1998, Ramage and Schiel 1999, Cowie *et al.* 2000, Boese 2002, Rossi *et al.* 2007, Schiel and Lilley 2007), rocky subtidal (Wernberg and Connell 2008), or subtidal unvegetated soft bottom communities (e.g. Rumohr *et al.* 1996, Kaiser *et al.* 2000, Powilleit *et al.* 2006, Smith *et al.* 2006). Currently, there are only a few studies on the effects of mechanical disturbance on nontidal vegetated soft bottom communities (e.g. Boström and Bonsdorff 2000, Herkül and Kotta 2009). Although macrophytes provide both habitat and food for a variety of benthic invertebrates in such communities, it is not uncommon that disturbance experiments exclude macrophytes. Studying both benthic macrovegetation and invertebrates allow us to demonstrate the links between disturbance, macrophytes, and invertebrates.

Coastal benthic communities in boreal environments are exposed to natural physical disturbances of varying magnitude caused mainly by storm events and ice scour. In sedimentary habitats, physical disturbance modifies sediment structure and seriously damages infauna and macrophytes and to a lesser extent epifauna (Boström and Bonsdorff 2000, Dernie *et al.* 2003). As invertebrates show a high degree of selectivity for a sediment structure and macrophyte species (Kotta and Orav 2001, Orav-Kotta and Kotta 2003, 2004), physical disturbance may also indirectly shift the structure and functioning of benthic communities. Disturbance causes a partial or total removal of dominant species creating unoccupied space for further colonization and may thus alter the dominance structure (Sousa 1984, Schiel and Lilley 2007). Strong levels of physical disturbance favours the dominance of opportunistic fast growing species and mobile epifauna (Sousa 1984, Pugh & Davenport 1997, van Dalfsen *et al.* 2000, Posey and Alphin 2002).

The coastal ecosystems of the northern Baltic Sea are very dynamic and characterised by high physical disturbance (Hällfors *et al.* 1981, Bonsdorff 2006). Similarly to other boreal ecosystems, strong storm events and ice scour are regarded as the most severe natural physical disturbances in shallow water areas (Hällfors *et al.* 1981, Kiirikki 1996, Idestam-Almquist 2000). In addition to natural physical disturbances, anthropogenic disturbances like boating and dredging activities and resource extraction are common in coastal areas (Sandström *et al.* 2005, Szymelfenig *et al.* 2006, Kotta *et al.* 2009a). The magnitude of mechanical disturbance in shallow water soft bottom communities in the northern Baltic Sea may range from a small impact that removes a few individuals to a total removal of a community caused by severe ice scour. The timing of disturbance is known to determine the nature of the effects on benthic communities (Sousa 1984, Benedetti-Cecchi and Cinelli 1994, Skilleter *et al.* 2006); e.g. the effect of a disturbance on a benthic community depends on the phase of macrobenthic seasonal succession in which the disturbance takes place (Kim and DeWreede 1996). Due to strong seasonality,

this is expected to be especially relevant in the Baltic Sea. Species diversity is low in the northern Baltic Sea and one functional group is often represented by a few or a single species (Kiirikki 1996, Bonsdorff and Pearson 1999, Bonsdorff 2006). Therefore, it is expected that physical disturbances may pose an additional challenge for the Baltic communities due to the presence of other stress factors such as low salinity and large temperature fluctuations (Segerstråle 1957, Kotta *et al.* 2008a). However, the Baltic species are tolerant to strong fluctuations in the physical environment (Bonsdorff 2006, Powilleit *et al.* 2006, Kotta *et al.* 2009a) and thus it is likely that they can easily cope with physical disturbance.

Shallow water vegetated soft bottom communities are widespread in the northern Baltic Sea and have an important role in the coastal ecosystems. These communities, dominated by phanerogams (e.g. *Potamogeton* spp., *Zannichellia palustris*) or charophytes, form an important habitat for a variety of benthic invertebrates and macrophytes (e.g. Boström and Bonsdorff 1997, Appelgren and Mattila 2005, Hansen *et al.* 2008). Vegetated shallow water soft bottoms generally provide feeding and nursery areas for several fish and bird species (Mattila *et al.* 1999, Grenouillet and Pont 2001, Heck *et al.* 2003, Sandström *et al.* 2005, Schmieder *et al.* 2006). Despite their importance, the role of physical disturbance on the development of such soft bottom communities remains largely unevaluated. There is evidence that, concurrent with the climate change, storms may become more frequent and violent (Woth *et al.* 2006). Consequently, mechanical disturbance may become more frequent and severer and thus have a greater effect on benthic communities.

In this paper, we studied the effects of physical disturbance (mimicking an ice scour or a severe storm) and the timing of disturbance (spring, summer) on the development of soft bottom macrovegetation and invertebrate communities in a shallow bay in the northern Baltic Sea. We hypothesize that (1) disturbance reduces the number of benthic species, (2) disturbance changes the abundances and biomasses of benthic species, and (3) the magnitude of impacts depend on the timing of disturbance.

Material and methods

Study site

The study was conducted in Kõiguste Bay (58°22.10´N 22°58.69´E), in the Gulf of Riga, in the northern Baltic Sea. Kõiguste Bay is a brackish, nontidal, semi-enclosed and shallow water basin. The prevailing sediment types in 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. The experiment was carried out in a shallow water area (1 m) where the bottom sediment was characterised by a layer of sand mixed with some pebbles on hard clay. The phytobenthic community was dominated by the higher plant *Potamogeton pectinatus*. Several green, brown, and red algal species like *Cladophora glomerata*, *Pilayella littoralis*, and *Ceramium tenuicorne* grew on higher plants and stones. The prevailing benthic invertebrates in the experimental area were the cockle *Cerastoderma glaucum*, the gastropods *Hydrobia ulvae* and *Theodoxus fluviatilis*, the polychaete *Hediste diversicolor*, and chironomid larvae.

Experimental design and sampling

The mechanical disturbance involved the removal of the upper sediment layer (ca. 3 cm) including the vegetation and benthic invertebrates. The sediment was removed from 1 m × 1 m quadrates with a sharp-edged hand net. The quadrates were marked with numbered stones. The excavated material was discarded at a distance of at least 25 m shoreward from the experimental area. Both disturbed and control plots were replicated six times. Treatments were randomly assigned to the quadrates. Experimental plots were established on 12 May 2005 (hereafter spring) and 20 July 2005 (hereafter summer). Immediately after the establishment of experimental quadrates, both disturbed and undisturbed (control) quadrates were sampled. Further sampling was done as follows: (1) quadrates established on 12 May 2005 were sampled on 20 July 2005 and on 20 Sep. 2005 (hereafter autumn); (2) quadrates estab-

lished in 20 July 2005 were sampled on 20 Sep. 2005. All comparisons for assessing the impact of disturbance were made between the disturbed and control quadrates sampled on the same date.

An Ekman type bottom grab sampler (0.02 m²) was used for sampling benthos. The grab sampler was manually operated by a diver to ensure representativness of samples. Benthos samples were sieved through a 0.25 mm mesh and the residuals were placed in plastic bags. The samples were stored deep frozen (–18 °C) until analysis. In the laboratory, all samples were sorted under a binocular microscope (20–40× magnification). All macrobenthic species were identified to the species level, except for oligochaetes, chironomids, and juveniles (size < 5 mm) of gammarid amphipods. Individuals of all taxa were counted and weighed. Prior to weighing, animals and plants were dried at 60 °C for 48 hours and two weeks, respectively. Abundances and biomasses were calculated per square metre.

Sediment samples for organic matter content were collected from quadrates using a cylindrical core (∅ 1.6 cm). Care was taken to avoid trapping animals and plants in the samples. 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).

Statistical methods

PERMANOVA (Anderson *et al.* 2008), based on Bray-Curtis dissimilarities, was used to test for differences in the abundance and biomass structure of benthic invertebrates and in the biomass structure of benthic macrophytes between disturbed and control plots during different periods. An abundance/biomass structure (= abundance/biomass dominance structure) is a multivariate community measure that involves both species composition and abundance/biomass of each species in a sample. Data was fourth-root-transformed prior to computing Bray-Curtis dissimilarities to down-weight the dominant species and increase the contribution of species with lower abundances or biomasses to the dissimilarities (Thorne *et al.* 1999, Anderson *et al.* 2008). Separate dissimilarity matrices were calculated for

zoobenthos abundance and biomass, and phytobenthos biomass. A PERMDISP procedure was performed to test for homogeneity of dispersions of dissimilarity data (Anderson *et al.* 2008). If PERMANOVA revealed differences between disturbed and control communities, a SIMPER (Clarke & Warwick 2001) analysis was performed on the fourth-root-transformed data to determine the contribution of individual taxa to the average dissimilarity between treatments. A non-metric multidimensional scaling (MDS; Clarke & Warwick 2001) on the fourth-root-transformed data was used to visualize differences in the structure of benthos. One-way factorial ANOVA (Hill and Lewicki 2007) was used to assess differences in organic matter content of sediment, species richness (number of benthic species), abundance and biomass of species, and functional groups for each sampling date. The data were tested for normality and homogeneity of variances before running ANOVA using a Kolmogorov-Smirnov test and Levene's test, respectively. The statistical package PRIMER (Clarke and Gorley 2006) was used to run PERMANOVA, SIMPER, and MDS. For ANOVA, the statistical package STATISTICA (StatSoft 2010) was used.

Results

Physical disturbance caused significant differences in the dominance structure of the benthic community immediately after the establishment of the experimental quadrates in spring (zoob-

enthos abundance and biomass, phytobenthos biomass; PERMANOVA, $p < 0.05$) but not in summer ($p > 0.05$). Nevertheless, disturbance immediately reduced the richness of benthic species and the abundances and biomasses of benthic species. However, the differences were statistically significant only in spring (Table 1). An extensive drifting algal mat was observed in the study area in summer. Owing to wave activity, the algal mat quickly spread to the newly established plots, thus, introducing most of the local species but at lower abundances and biomasses compared to the control plots.

The springtime disturbance affected the biomass structure of phytobenthos (PERMANOVA, $p = 0.034$) and zoobenthos ($p = 0.021$) and the abundance structure of zoobenthos ($p = 0.004$) in summer (MDS plots in Fig. 1) but not in autumn. The summertime disturbance had no effect on the community structure in autumn (PERMANOVA: $p > 0.05$; Table 2)

Hediste diversicolor, lepidopteran and chironomid larvae, and idoteid isopods contributed most to the overall dissimilarity of zoobenthos abundance structure between the disturbed and control plots that were established in spring and sampled in summer (SIMPER test, Table 3). In general, disturbance reduced species abundances. Unlike most other species, chironomid and lepidopteran larvae, *H. diversicolor*, and juvenile gammarids had higher abundances and biomasses in the disturbed plots than in the control plots. *Macoma balthica*, *Cerastoderma glaucum*, and *H. diversicolor* contributed most to the overall difference in the biomass of zoo-

Table 1. The differences in community variables between the disturbed and control plots immediately after the establishment of the experimental plots as revealed by ANOVA. Significant results are set in boldface. df = 1 for all variables.

| Community variable	Spring				Summer			
	Disturbed	Control	*F*	*p*	Disturbed	Control	*F*	*p*
Zoobenthos								
Species number	4.20	7.00	**6.88**	**0.031**	6.30	8.70	0.47	0.530
Total abundance (ind. m⁻²)	1908.20	6185.20	**10.97**	**0.011**	7896.00	15745.00	2.65	0.179
Total biomass (g m⁻²)	11.47	32.18	**9.46**	**0.015**	60.51	115.13	2.01	0.229
Phytobenthos								
Species number	6.00	9.00	**15.00**	**0.005**	12.00	14.00	0.34	0.590
Total biomass (g m⁻²)	4.40	50.65	**14.66**	**0.005**	25.87	70.64	3.92	0.119
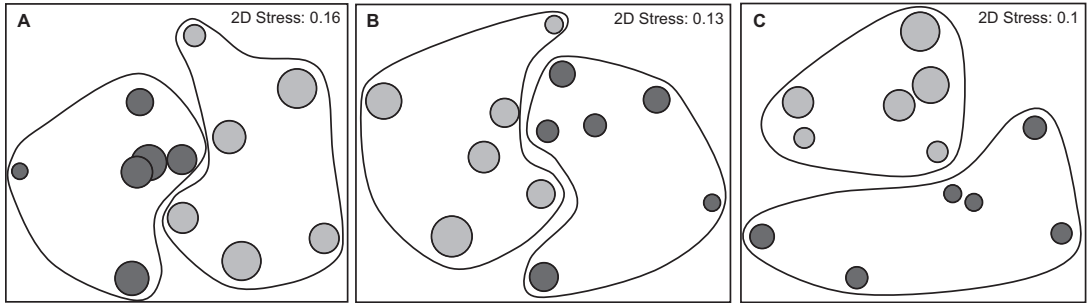
Fig. 1. nMDS ordination (Bray-Curtis similarities of fourth-root transformed data) of zoobenthos (**A**) abundance and (**B**) biomass, and (**C**) phytobenthos biomass in the quadrates established in spring and sampled in summer. Light grey = control plots, dark grey = disturbed plots. The relative size of the circles indicates the total abundance or total biomass of benthic organisms in a sample.

benthos between disturbed and control plots. Physical disturbance increased the biomass of *M. balthica* and *H. diversicolor* and reduced the biomass of *C. glaucum*. *Potamogeton pectinatus*, *Zannichellia palustris*, and *Fucus vesiculosu*s (drifting plants and fragments) contributed the most to the overall difference in the phytobenthos biomass between disturbed and control plots. Generally, disturbance reduced the biomass of plant species; however, it facilitated the growth of *Chara canescens* and accumulation of drifting *F. vesiculosus* (Table 3).

The springtime disturbance affected the univariate characteristics (e.g. species number and total biomass) of the phytobenthos community in summer, but the effect did not last until autumn (ANOVA, Table 4). The species number and total biomass of phytobenthos, biomass of vascular plants, and green algae were lower in the physically disturbed plots than in the control plots (Table 4). The springtime disturbance also influenced the zoobenthos characteristics; however, in contrast to that of phytobenthos, the zoobenthos characteristics (except for the

abundance of suspension feeders) did not differ among the treatments in summer, but it did in autumn (Table 4). When differences were significant, disturbance always reduced the values of the univariate characteristics. Only charophytes tended to be facilitated by disturbance ($p = 0.096$). The summertime disturbance affected none of the zoobenthic and phytobenthic univariate characteristics. Furthermore, disturbance had no effect on the content of organic matter in the sediment (ANOVA: $p > 0.05$; Table 4).

Discussion

This study showed that stronger impacts of physical disturbance on benthic communities are expected when disturbance takes place at an early stage of the seasonal succession of macrobenthic communities as compared with a disturbance at a mid-stage of the seasonal succession of macrobenthic communities. This is in disagreement with recent findings on the response of a brackish water charophyte community to mechanical

Table 2. The differences in benthos structure between the disturbed and undisturbed plots in different periods as revealed by PERMANOVA. Significant results are set in boldface. Each test was done using 9999 permutations. df = 1 for all periods.

Period	Zoobenthos abundance			Zoobenthos biomass			Phytobenthos biomass		
	MS	pseudo *F*	*p*	MS	pseudo *F*	*p*	MS	pseudo *F*	*p*
Spring–summer	923.10	**2.43**	**0.004**	877.41	**2.19**	**0.021**	2488.50	**2.93**	**0.034**
Spring–autumn	490.90	1.74	0.110	508.67	1.75	0.096	954.96	1.00	0.443
Summer–autumn	78.51	0.35	0.959	140.07	0.51	0.856	787.05	1.50	0.213

Table 3. Results of the SIMPER test (fourth-root-transformed data) for identifying taxonomic contributions to the overall dissimilarity between the disturbed and control plots established in spring and sampled in summer. Average abundance or biomass (fourth-root-transformed) in the disturbed and control plots, average dissimilarity (Av. diss.), contribution to the average dissimilarity (Contrib.), and cumulative contribution (Cum. contrib.) are shown for each taxon. Taxa that cumulatively contributed less than 10% to the overall difference were excluded from the table. Invertebrate feeding group indicated in parentheses: C = carnivore, D = deposit feeder, H = herbivore, S = suspension feeder.

Species	Disturbed	Control	Av. diss.	Contrib. (%)	Cum. contrib. (%)
Zoobenthos abundance					
Hediste diversicolor (D)	3.23	2.47	2.47	8.22	8.22
Lepidoptera (C)	1.83	0.00	2.35	7.85	16.07
Idotea chelipes (H)	1.75	2.34	2.28	7.59	23.66
Chironomidae (D)	4.47	3.68	2.24	7.46	31.13
Idotea balthica (H)	0.00	1.61	2.07	6.91	38.03
Theodoxus fluviatilis (H)	4.95	5.83	1.83	6.10	44.14
Mytilus trossulus (S)	0.44	1.39	1.77	5.89	50.03
Hydrobia ulvae (H)	9.38	9.83	1.70	5.66	55.69
Gammarus juv. (H)	1.31	0.87	1.70	5.65	61.34
Macoma balthica (D)	0.96	0.96	1.68	5.61	66.95
Radix balthica (H)	3.04	4.24	1.67	5.58	72.53
Gammarus salinus (H)	0.00	1.31	1.58	5.28	77.81
Cerastoderma glaucum (S)	3.62	4.45	1.22	4.05	81.86
Odonata (C)	0.87	0.00	1.13	3.76	85.62
Plecoptera (C)	0.00	0.96	1.12	3.73	89.35
Trichoptera (C)	0.00	0.57	0.62	2.05	91.40
Zoobenthos biomass					
Macoma balthica (D)	0.51	0.42	3.07	10.15	10.15
Cerastoderma glaucum (S)	1.76	2.30	3.02	9.99	20.15
Hediste diversicolor (D)	0.76	0.70	2.49	8.23	28.37
Theodoxus fluviatilis (H)	1.59	1.88	2.41	7.98	36.36
Radix balthica (H)	1.03	1.38	2.39	7.90	44.26
Lepidoptera (C)	0.47	0.00	2.18	7.21	51.47
Idotea chelipes (H)	0.26	0.45	1.73	5.71	57.18
Idotea balthica (H)	0.00	0.35	1.67	5.51	62.70
Odonata (C)	0.36	0.00	1.63	5.39	68.09
Hydrobia ulvae (H)	2.14	2.34	1.47	4.87	72.96
Chironomidae (D)	0.55	0.35	1.33	4.40	77.36
Gammarus salinus (H)	0.00	0.22	1.01	3.34	80.70
Mytilus trossulus (S)	0.08	0.19	1.00	3.30	84.00
Plecoptera (C)	0.00	0.24	1.00	3.30	87.30
Gammarus juv. (H)	0.17	0.15	0.97	3.20	90.50
Phytobenthos biomass					
Potamogeton pectinatus	1.30	1.87	5.72	12.34	12.34
Zannichellia palustris	0.82	1.52	5.00	10.80	23.14
Fucus vesiculosus	1.32	0.36	4.49	9.69	32.83
Chara canescens	1.25	0.32	4.15	8.95	41.78
Furcellaria lumbricalis	0.44	1.09	3.62	7.81	49.59
Myriophyllum spicatum	0.60	1.27	3.55	7.65	57.24
Cladophora glomerata	0.71	1.41	2.77	5.98	63.23
Pilayella littoralis	0.95	1.38	2.43	5.25	68.48
Tolypella nidifica	0.54	0.82	2.21	4.77	73.25
Sphacelaria arctica	0.58	1.02	1.79	3.87	77.11
Dictyosiphon foeniculaceus	0.40	0.67	1.73	3.75	80.86
Ceramium tenuicorne	0.85	1.09	1.60	3.46	84.32
Polysiphonia fucoides	0.14	0.45	1.34	2.88	87.20
Ulva intestinalis	0.17	0.34	1.19	2.57	89.76
Stictyosiphon tortilis	0.04	0.29	1.06	2.29	92.05

disturbance. In an experiment conducted by Torn *et al.* (2010), the timing of disturbance had a significant effect on the charophyte community but with stronger effects when disturbed during the mid-stage of seasonal succession as compared with the early-stage of seasonal succession of macrobenthic communities. It is possible that the early-stage disturbance postponed the development of charophyte communities and, therefore, had no long lasting seasonal effects. In the present study area, phanerogams dominated the macrophyte community. Disturbance applied at the early succession removed phanerogams and facilitated charophytes.

Drifting algal mats harbouring diverse macrofaunal communities are common in the experimental (Lauringson and Kotta 2006) and neighbouring areas in the northern Baltic Sea (Norkko *et al.* 2000, Kotta *et al.* 2008b). Such mats were also observed in the experimental area in the summer and autumn. Even with a low wave energy, the algal mat quickly dislocated and spread to the newly established plots. The facilitative effect of drifting algal mats on the spread of benthic species may explain why the summertime disturbance did not cause significant changes in the community immediately after setting up the experimental plots. The algal mat was not present in spring, and the springtime disturbance had an effect on the community immediately after disturbance and continued to have an effect later on. Thus, the drifting algal mats may be regarded as an efficient vector for spreading species (Norkko *et al.* 2000, Arroyo *et al.* 2006, Lauringson and Kotta 2006) and they may contribute to the recovery of a benthic community after disturbance.

This experiment showed that the benthic community composition recovered within a vegetation period. The experimental plots that were disturbed in spring clearly differed from the control community in summer but not in autumn. However, the univariate community characteristics showed a different pattern. The summertime phytobenthos characteristics (e.g. species number, total biomass, biomass of vascular plants) were significantly affected by the springtime disturbance; whereas in the case of zoobenthos characteristics, only the abundance of suspension feeders significantly dif-

Table 4. The differences in community variables and organic matter content of sediment due to disturbance as revealed by ANOVA. Significant results are set in boldface. Decrease in the value of a variable was observed for all significant differences. df = 1 for all variables.

Community variable	Spring–summer		Spring–autumn		Summer–autumn	
	F	*p*	*F*	*p*	*F*	*p*
Species number of zoobenthos	0.16	0.695	1.00	0.341	0.07	0.804
Total abundance of zoobenthos	0.79	0.395	**15.63**	**0.003**	0.39	0.549
Total biomass of zoobenthos	4.02	0.073	**13.50**	**0.004**	0.37	0.558
Abundance of herbivores	0.80	0.393	**5.74**	**0.038**	0.28	0.611
Abundance of deposit feeders	0.18	0.685	0.25	0.627	0.70	0.423
Abundance of suspension feeders	**7.37**	**0.022**	**10.59**	**0.009**	0.18	0.683
Abundance of carnivores	0.13	0.724	0.69	0.425	0.31	0.591
Biomass of herbivores	3.13	0.108	4.39	0.063	2.39	0.153
Biomass of deposit feeders	0.33	0.578	2.88	0.120	0.24	0.638
Biomass of suspension feeders	3.60	0.087	1.95	0.192	0.02	0.897
Biomass of carnivores	2.11	0.177	1.63	0.231	1.92	0.196
Species number of phytobenthos	**8.62**	**0.015**	0.47	0.511	2.43	0.150
Total biomass of phytobenthos	**6.91**	**0.025**	1.18	0.303	0.21	0.656
Biomass of vascular plants	**9.25**	**0.012**	1.41	0.262	0.01	0.926
Biomass of green algae	**58.22**	**< 0.001**	0.02	0.906	0.78	0.399
Biomass of brown algae	0.15	0.709	0.10	0.763	2.05	0.183
Biomass of red algae	1.80	0.210	0.07	0.796	0.28	0.609
Biomass of charophytes	3.38	0.096	–	–	–	–
Organic matter content of sediment	0.16	0.701	0.43	0.525	0.20	0.668

fered between the control and disturbed plots (Table 4). By autumn, there were no significant differences in phytobenthos variables due to the springtime disturbance. Contrastingly, in autumn, the total abundance and biomass of zoobenthos and abundance of herbivores significantly differed between the control and disturbed plots due to the springtime disturbance (Table 4). This indicates that the species composition and the distribution pattern of abundance and biomass between zoobenthic species returned to normal faster than the total abundance and biomass of all the species. Additionally, it seems that a statistically significant difference takes more time to emerge in zoobenthos abundance and biomass as a result of the springtime disturbance. The abundance and biomass of zoobenthos were higher in autumn as compared with those in summer which possibly explains the appearance of the effect of the springtime disturbance in autumn but not in summer.

The springtime disturbance significantly reduced the number of phytobenthos species in summer. The disturbance decreased the biomass of both vascular plants and green algae. In addition to the direct effect of the disturbance, the removal of vascular plants, that provide a secondary substratum for epiphytes, contributed to a loss of phytobenthos species richness and to a decrease of the biomass of green algae. Macrophytes are known to host a high diversity and density of epiphytes in the Baltic Sea (Wikström and Kautsky 2007, Kostamo 2008) and elsewhere (Fredriksen *et al.* 2005, Christie *et al.* 2009). The disturbance had an immediate effect on the number of zoobenthos species only in spring and no significant differences were detected in the later samplings. Most of the species in the Baltic Sea are regarded as highly tolerant to disturbances. Species inhabiting shallow coastal areas are exposed to high levels of mechanical disturbances caused by severe storms and ice scour and are, therefore, capable of quick recovery through high mobility of adult organisms, larval settlement, or vegetative growth (Posey and Alphin 2002, Negrello Filho *et al.* 2006, Powilleit *et al.* 2006, Skilleter *et al.* 2006, Smith *et al.* 2006). The mobility together with the facilitative effect of drift algal mats may have contributed to the establishment of invertebrate species in the disturbed experimental plots. Additionally, we infer that a further increase of invertebrate abundance and biomass, reaching the control values, takes more time than the recovery of the species composition.

Univariate community measures indicated that phytobenthos responded more quickly to the disturbance and recovered faster as compared with zoobenthos. This is in accordance with the successional pattern in the area; i.e., zoobenthos, being directly or indirectly dependent on phytobenthic production, follows the peak of phytobenthos (Kotta *et al.* 2009b, Nordström *et al.* 2009). Biomasses of aquatic plants, mesoherbivores, and deposit feeders are positively correlated in many water bodies as plants provide benthic invertebrates with a habitat and food resources (Huntly 1991, Kotta and Orav 2001, Orav-Kotta and Kotta 2004, Kotta *et al.* 2009b). Animals respond more strongly to the amount of available resource than to the diversity of plants that provide it (Kotta *et al.* 2006). This assertion may explain the slow recovery of the total invertebrate abundance and biomass, even though the species composition of macroalgal community did not vary among treatments.

Charophytes were the only group of plants that tended to be facilitated by the disturbance in spring. During the summer sampling, the charophyte biomass was higher in the disturbed plots than in the control plots. This pattern may be related to the timing of the disturbance and the seasonal succession of a phytobenhic community. The spring disturbance took place before the seasonal appearance of charophytes and removed competitively superior *Potamogeton pectinatus*, therefore, giving an advantage to the growth of charophytes (Van den Berg *et al.* 1998). Charophytes have been found to suffer more from eutrophication than vascular plants (Blindow 1992, Van den Berg *et al.* 1998). Thus, the physical disturbance in spring (e.g. ice scour) that removes vascular plants may counteract the negative effect of eutrophication on charophytes.

In our study, we investigated the role of a small scale disturbance on a benthic community. Natural disturbances may also occur at much larger spatial and temporal scales which are impossible to apply in experimental designs. Small scale experimental studies combined with the results of observational studies on natural

disturbances may help us to gain better understanding of the ecological role of disturbances at different spatial and temporal scales. Recent climate change is expected to increase storminess and raise the importance of physical disturbance in the dynamics of coastal benthic communities. In the perspective of coastal zone management, our current study indicates that springtime physical disturbances, e.g. in connection with maritime construction activities, should be avoided in the coastal sea.

To conclude, (1) disturbance reduced phytobenthos species richness, (2) disturbance reduced benthic abundances and biomasses, but the species composition recovered faster than the abundances and biomasses of benthic organisms, (3) the magnitude of impact depended on the timing of disturbance with a springtime disturbance having stronger effects on the benthic community than a summertime disturbance.

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