DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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# KRISTJAN HERKÜL

# Effects of physical disturbance and habitat-modifying species on sediment properties and benthic communities in the northern Baltic Sea

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# LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following papers, which are referred to in the text by Roman numerals:

I. Herkül K., Kotta J. & Pärnoja M. Effect of physical disturbance on the soft sediment benthic macrophyte and invertebrate community in the northern Baltic Sea. Boreal Environmental Research, 16 (in press).

II. Herkül K. & Kotta J. 2009. Effects of eelgrass (*Zostera marina*) canopy removal and sediment addition on sediment characteristics and benthic communities in the northern Baltic Sea. Marine Ecology, 30 (Suppl. 1), 74–82.

III. Herkül K., Kotta J., Kotta I. & Orav-Kotta H. 2006. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. Oceanologia, 48 (S), 267–282.

IV. Kotta J., Herkül K., Kotta I., Orav-Kotta H. & Lauringson V. 2009. Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associate invertebrate community. Marine Ecology, 30 (Suppl. 1), 56–64.

V. Kotta J., Herkül K., Kotta I., Orav-Kotta H. & Aps R. 2009. Response of benthic invertebrate communities to the large-scale dredging of Muuga Port. Estonian Journal of Ecology, 58, 286–296.

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*** – complete contribution (100 %)
** – leading contribution (> 50 %)
* – supporting contribution (< 50 %)

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# 1. INTRODUCTION

Disturbance is a key factor regulating the structure and functioning of natural communities and causing spatial and temporal heterogeneity (Sousa 1984, Pickett & White 1985, Whitlatch *et al.* 1998, Zajac *et al.* 1998, Widdicombe & Austen 2001, Dernie *et al.* 2003). There are different definitions of disturbance. Grime (1977) described disturbance as partial or total destruction of biomass by consumers, pathogens, or physical forces. Pickett & White (1985) have a broader definition where disturbance is "any discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substratum availability, or the physical environment". Additionally, Sousa (1984) emphasised the importance of disturbance in creating opportunities for new individuals to become established. On the basis of the causative agent, physical and biological disturbances can be distinguished (Hall 1994, Sousa 2001). Biological disturbance includes consumption of prey by predators and grazers, deaths of parasitised hosts, nonpredatory behaviours that inadvertently kill or displace other organisms, bioturbation (reworking and resuspension of soft sediments by burrowing infauna) (Sousa 1984, Hall 1994, Sousa 2001). Physical disturbance in subtidal marine environments includes abrasion by waves and currents, ice scour, burial under sediments, abnormally high or low water temperature or salinity, hypoxia, landslides, lava flows, and tectonic activity that uplifts surface (Sousa 1984, Hall 1994, Sousa 2001). In addition to natural physical disturbances, anthropogenic disturbances like boating, dredging and disposal of dredged material, underwater construction, resource extraction, and bottom trawling are common in coastal areas (Hall 1994, Thrush *et al.* 1995, Sandström *et al.* 2005, Szymelfenig *et al.* 2006).

Local physical disturbances may have also global causes. Global climate change may result in altered disturbance regimes. There is evidence that, concurrent with the climate change, storms may become more frequent and violent (Woth *et al.* 2006). Recent shifts in climate conditions have resulted in elevated winter temperatures and reduced the extent and duration of ice cover in northern Europe (Jaagus 2006). Consequently, mechanical disturbances may become more frequent and severer and thus have a greater damaging effect on ecosystems than earlier.

As disturbance events are unevenly distributed in space and time, a mosaic of patches is generated at different stages in a successional sequence (Connell 1978, Pickett & White 1985, Hall 1994). This mosaic of patches is important in maintaining species diversity by preventing the competitive exclusion by dominant species in an assemblage (intermediate disturbance hyopthesis; Connell 1978). The intermediate disturbance hypothesis states that species richness is highest when disturbances are intermediate with respect to both frequency and intensity of disturbance. When disturbances are very intense or very frequent, only the most resistant species are able to survive, while too weak or too rare disturbances fail to impair the competitively superior species (Connell 1978).

Most habitats are generated by the presence of a single or a few habitat-modifying species that alter local environmental conditions (Bruno & Bertness 2001, Stachowicz 2001). Habitat-modifying species contribute to the habitat complexity and create refuge from physical and biological disturbances and predation (Heck & Wetstone 1977, Bruno & Bertness 2001). Habitat-modifying species may change the physical structure of seabed and alter the cycling and state of materials (Jones *et al.* 1994). Typical examples of habitat-modifying species in marine environments include species of submerged macrophytes, mussels, and corals (Jones *et al.* 1994, Bruno & Bertness 2001). Habitat-modifying species, especially canopy algae, are known to mitigate the stress caused by physical disturbances in intertidal systems (*e.g.* Dayton 1975, Leonard 1999), but the knowledge is scarce on the interactive effects of the habitat-modifying species and physical disturbances in subtidal or non-tidal environments.

Numerous studies on physical disturbances in marine environments have focused either on intertidal systems (*e.g.* Kim & DeWreede 1996, Hall & Harding 1997, Keough & Quinn 1998, Ramage & Schiel 1999, Cowie *et al.* 2000, Boese 2002, Rossi *et al.* 2007, Schiel & Lilley 2007), rocky subtidal (Wernberg & 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). Removal experiments of habitat-modifying species have been carried out mainly in intertidal habitats (*e.g.* Benedetti-Cecchi & Cinelli 1992, Jenkins *et al.* 2004, Lilley & Schiel 2006). Currently there are only a few studies on the effects of mechanical disturbance on subtidal or nontidal vegetated soft bottom communities (*e.g.* Boström & Bonsdorff 2000, Torn *et al.* 2010). 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. There are many observational studies that compare benthic communities among vegetated and unvegetated areas (*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 vegetation because differences can be due to factors other than vegetation.

The coastal ecosystems of the northern Baltic Sea are very dynamic and characterised by high physical disturbance (Hällfors *et al.* 1981, Bonsdorff 2006, Kotta *et al.* 2008a). 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). 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 effects on benthic communities (Sousa 1984, Benedetti-Cecchi & Cinelli 1994, Skilleter *et al.* 2006); for example the effect of a disturbance on a benthic community depends on the phase of macrobenthic seasonal succession in which it takes place (Kim & DeWreede 1996). Due to strong seasonality, the timing of disturbance 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 & 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) and thus it is likely that they can easily cope with physical disturbances.

Phanerogams (*e.g. Zostera marina* L., *Potamogeton* spp.) and charophytes (*e.g. Chara aspera* Willd., *Chara canescens* Desv. et Loisel.) are the most important habitat-modifying species on the shallow water soft bottoms of the northern Baltic Sea (Boström & Bonsdorff 1997, Schubert & Blindow 2003, Gustafsson & Boström 2009, Hansen *et al*. 2010) while *Fucus vesiculosus* L. and other macroalgae and the suspension-feeding mussel *Mytilus trossulus* Gould are important habitat-modifying species on hard bottoms (Norling & Kautsky 2007, Norling & Kautsky 2008, Wikström & Kautsky 2007). In addition to macrophytes, infauna modifies sedimentary habitats by bioturbation that influences mineralisation and distribution of organic matter in sediment, granulometrical and chemical composition of sediment, and resuspension (Karlson *et al*. 2005, Michaud *et al*. 2005, Gray & Elliott 2009).

Vegetated soft bottom communities are widespread in the northern Baltic Sea and have an essential role in the coastal ecosystems. These communities form an important habitat for a variety of benthic invertebrates and macrophytes in the Baltic Sea and elsewhere (*e.g.* Orth *et al*. 1984, Boström & Bonsdorff 1997, Appelgren & Mattila 2005, Hansen *et al*. 2008). Vegetated soft bottoms provide feeding and nursery areas for several fish and bird species (Mattila *et al*. 1999, Grenouillet & Pont 2001, Heck *et al*. 2003, Sandström *et al*. 2005, Schmieder *et al*. 2006). Moreover, soft bottom vegetation is known to stabilise the seabed in which they grow, reduce the resuspension of sediments, influence sediment deposition and compositon (Terrados & Duarte 2000, Gacia *et al*. 2003, Bos *et al*. 2007, Hendriks *et al*. 2008, Hasegawa *et al*. 2008), and release oxygen into the sediment (Enríquez *et al*. 2001, Frederiksen & Glud 2006).

The suspension-feeding mussels such as *Mytilus trossulus* are important habitat-modifying species in several aspects. By feeding on phytoplankton, mussels bring additional nutrients to the benthic system (Officer *et al*. 1982). By increasing habitat complexity, they support higher diversity of associated benthic organisms (Aldridge *et al*. 2007, Norling & Kautsky 2007, Sardiña *et al*. 2008). Finally, mussel beds and empty shells provide secondary hard substratum on soft bottoms (Albrecht 1998).

Despite their importance, the separate and interactive effects of physical disturbance and habitat-modifying species on subtidal benthic communities have remained largely unevaluated.

## Objectives

The general aim of this thesis was to study the effects of physical disturbance and habitat-modifying species on sediment properties and benthic communities in the northern Baltic Sea. The specific objectives were to study:

- the effects of various physical disturbances (sediment removal and addition, wave exposure, dredging activities) on the structure of macrobenthic communities (**I, II, III, IV, V**);
- the effects of habitat-modifying benthic invertebrate and macrophyte species on the structure of macrobenthic communities (**II, III, IV**) and sediment properties (**II)**;
- the effects of physical disturbances on sediment properties (**I**, **II**);
- the effect of the timing of disturbance on the development of macrobenthic community (**I**).

# 2. MATERIAL AND METHODS

## 2.1. Study area

The studies for this thesis were conducted in the northern Gulf of Riga (**I, III, IV**) and southwestern Gulf of Finland (**II, V**), Baltic Sea (Fig. 1). The Gulf of Riga is situated in the northern Baltic Sea and is a relatively shallow water body. The gulf is connected to the Baltic Proper via narrow straits. The Gulf of Riga receives fresh water from a huge drainage area and therefore has reduced salinity at 5.0–6.5 psu. In general, the bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the gulf is characterised by a wide coastal zone with diverse bottom topography and sediments. Kõiguste Bay (**I, III, IV**) is located in the northern Gulf of Riga. The water depths of the bay are typically between 1 and 4 m. The average salinity is 5 psu. The prevailing sediments in the bay are clayey sand mixed with pebbles and gravel. The area is influenced by a diffuse nutrient load from the moderately eutrophicated Gulf of Riga (Kotta *et al.* 2008a). The soft bottom phytobenthic community is dominated by the higher plant *Potamogeton pectinatus*. Several green, brown, and red algal species such as *Cladophora glomerata* (L.) Kütz., *Pilayella littoralis* (L.) Kjellm., and *Ceramium tenuicorne* (Kützing) Waern grow on higher plants and stones. The prevailing benthic invertebrates in the experimental area are the bivalves *Cerastoderma glaucum* (Bruguière) and *Macoma balthica* (L.), the gastropods *Hydrobia ulvae* (Pennant) and *Theodoxus fluviatilis* (L.), the polychaete *Hediste diversicolor* (O.F. Müller), and chironomid larvae. Extensive proliferation of ephemeral macroalgae has been reported in the area (Martin *et al.* 2003, Paalme 2005). At the later stages of annual succession drift algal mats may form in shallow areas (Lauringson & Kotta 2006).

Compared to the Gulf of Riga, the Gulf of Finland is a much deeper basin with a good connection to the Baltic Proper. The average salinity in the Prangli experiment area (**II**) is 6 psu. Sand and gravel dominate, but standalone stones are also found in shallow waters. The area is strongly influenced by currents and wave action. The phytobenthic community is dominated by the eelgrass *Zostera marina* followed by the brown alga *Pilayella littoralis* and the red alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux. The bivalves *Macoma balthica* and *Mytilus trossulus*, amphipods *Corophium volutator* (Pallas) and *Gammarus* spp. and the gastropod *Hydrobia ulvae* are the dominating invertebrates. Meadows of *Z. marina* prevail in the depth range of 2–5 m.

Muuga Bay (**V**) is relatively exposed to the sea. The prevailing depths are between 5 and 40 m, and seabed sediments consist mainly of clay, silt, and fine to medium sands. Hard substrates (pebbles and boulders) are located in the vicinity of peninsulas and cover a small area. Salinity values resemble those of the Prangli area. The phytobenthic community is poorly developed. Among benthic invertebrates the bivalves *Macoma balthica* and *Mytilus trossulus* prevail.

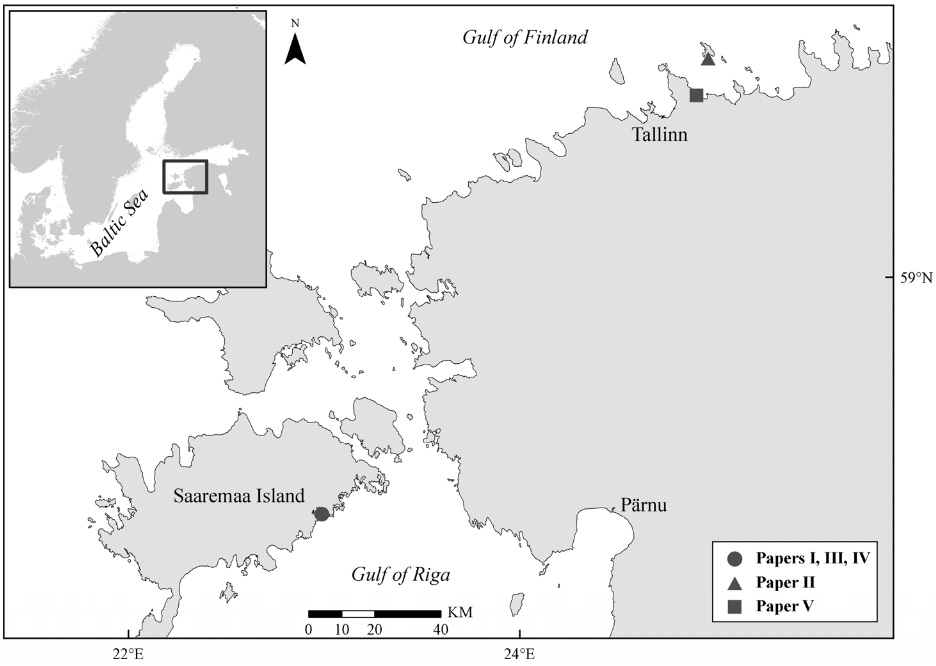

**Figure 1.** Study area.

## 2.2. Study designs

**Effect of physical disturbance on the soft sediment benthic macrophyte and invertebrate community** (**I**) was studied in Kõiguste Bay (58.368ºN 22.982ºE), the Gulf of Riga (Fig. 1). An *in situ* experiment was conducted 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 experiment was carried out in May–September 2005. The phytobenthic community was dominated by the higher plant *Potamogeton pectinatus*. The mechanical disturbance consisted in the removal of the upper sediment layer (ca. 3 cm) together with vegetation and benthic invertebrates from 1 m × 1 m quadrates. Both disturbed and control plots were replicated six times resulting in a total of 12 experimental plots. Experimental plots were established in May and July 2005. Immediately after the establishment of experimental quadrates, both disturbed and undisturbed (control) quadrates were sampled. The further sampling was done as follows: (1) quadrates established in May were sampled in July and September; (2) quadrates established in July were sampled in September. All comparisons for assessing the impact of disturbance were made between disturbed and control quadrates sampled on the same date. An Ekman type bottom grab sampler (0.02 $m^2$) was used for sampling benthos. Sediment samples for organic matter content were collected from quadrates using a cylindrical core (Ø 1.6 cm).

**Effects of the removal of the eelgrass (*Zostera marina*) canopy and sediment addition on sediment characteristics and benthic communities (II)** were experimentally studied near Prangli Island (59.610ºN, 25.004ºE), the Gulf of Finland (Fig. 1). The average biomass of the aboveground parts of *Zostera marina* in the experimental area was 58.0 ± 11.2 g dw $m^{-2}$ and the length of the leaves reached 40 cm. An *in situ* experiment was carried out in July–August 2006. The 50 cm × 50 cm experimental plots were placed in a natural *Z. marina* bed at 4 m depth. The experimental design included two treatments: canopy removal (manual removal of *Z. marina*) and sediment addition (two centimetres of natural seabed sediment). This 2 × 2 factorial design was replicated three times resulting in a total of 12 experimental plots. Oxygen flux through sediment-water interface, sediment granulometry and sediment organic matter content were measured four times: immediately after setting up the experimental plots and three times thereafter with 2–3 weeks intervals. Transparent cores (Ø 3.6 cm) were used to measure the oxygen flux and to sample sediment for granulometric and organic content analyses. The cores were inserted into sediment to a depth of 10 cm and the upper ends of the cores were closed with rubber stoppers. Oxygen concentrations in the cores were measured before and after 2.5 h incubation using an oxygen meter. Samples for macrobenthos community were collected only during the last sampling using a 10.3 cm diameter core.

**Effects of key invertebrate species and wave exposure on benthic communities (III, IV)** were studied in two *in situ* mesocosm experiments in Kõiguste Bay, northern Gulf of Riga (Fig. 1). Plastic buckets filled with defaunated sediment were used. The first experiment (June–July 2003, **III**) was aimed at studying the effects of the initial invertebrate community composition and wave exposure on the colonisation and further development of benthic communities. The suspension feeder *Cerastoderma glaucum*, the deposit feeder *Macoma balthica* and the herbivore *Theodoxus fluviatilis* were seeded into the buckets. All possible combinations of *C. glaucum*, *M. balthica* and *T. fluviatilis* and additional controls without animals served as the treatment of the initial invertebrate community (**III**). The buckets were sampled for macrobenthos at the end of the experiment (**III**). In the second experiment (June–September 2004, **IV**), the presence of the suspension feeding mussel *Mytilus trossulus*, substrate type (soft bottom with high organic content, soft bottom with low organic content, hard bottom), and wave exposure were manipulated. The buckets were sampled for macrobenthos monthly from June to September; separate sets of buckets were established at the beginning of the experiment to be sampled in subsequent months. In both experiments the wave exposure was manipulated by placing half of the buckets to an exposed area and the others to a sheltered area of Kõiguste Bay (**III**, **IV**). Three replicates of each treatment combination were deployed in both experiments. All bucket contents were analysed for macrobenthos.

**Response of benthic invertebrate communities to the large-scale dredging of Muuga Port** (**V**) was studied in the vicinity of Muuga Port, the Gulf of Finland (Fig. 1), in 2002–2007. This time series covered years before the large-scale dredging, the year of dredging (2004), and a period after the dredging. Altogether 10 stations in the depth range of 5.5–30 m were sampled every year using an Ekman type bottom grab sampler (0.02 $m^2$).

## 2.3. Sample analysis

**Macrobenthos** samples (**I–V**) were sieved in the field through a 0.25 mm mesh and the residuals were stored deep frozen 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 juveniles (size < 5 mm) of gammarid amphipods (identified to the genus level), oligochaetes (identified to the subclass level), and insect larvae (identified to the family or higher level). Dry biomass (60° C for 2 weeks) of each plant taxon and dry biomass of each animal taxon were measured (precision 0.0001 g). Abundance of each animal taxon was counted. Abundances and biomasses were calculated per square metre.

**The organic matter content of sediment** (**I, II, V**) was measured as a percentage loss of weight on ignition (500 ºC, 3 h) of dry sediment (60 ºC, 7 days).

For **granulometric analysis** (**II**) dry sediment (60 ºC, 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 was weighed (precision 0.001 g).

## 2.4. Statistical methods

For testing differences in the univariate measures standard ANOVA (**I, II, III, V**) or repeated measures ANOVA (**IV**) were used. For ANOVAs, statistical package STATISTICA (StatSoft 2010) was used. PERMANOVA (Anderson *et al.* 2008; **I, II**) or ANOSIM (Clarke & Warwick 2001; **III, V**) 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 treatment groups or years. SIMPER (Clarke & Warwick 2001) analysis was used to determine the contribution of individual taxa to the average dissimilarity between treatments (**I, III**). Non-metric multidimensional scaling (MDS; Clarke & Warwick 2001) on the fourth root transformed data was used to visualise differences in the structure of benthos (**I, II, III**). BEST analysis (BIOENV procedure) (Clarke & Warwick 2001) was used to relate the patterns of environmental variables to the structure of the benthic community (**V**).

# 3. RESULTS AND DISCUSSION

**Mechanical removal of sediment (I)** had varied effects on the benthic community but no effect on the sediment organic matter content. Physical disturbance caused significant differences in the dominance structure of the benthic community immediately after the establishment of the experimental quadrates in spring (zoobenthos abundance and biomass structure, phytobenthos biomass structure) but not in summer. Nevertheless, disturbance immediately reduced the species richness and densities of benthic species. However, the differences were statistically significant only in spring. An extensive drifting algal mat was observed in the study area in summer. Drifting algal mats harbouring diverse macrofaunal communities are common in the experimental (Lauringson & Kotta 2006) and neighbouring areas in the northern Baltic Sea (Norkko *et al.* 2000, Vahteri *et al.* 2000, Kotta *et al.* 2008b). Such mats were also observed in the experimental area in summer–autumn. 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 the experimental plots were set up and in autumn sampling. The algal mat was not present in spring and the springtime disturbance had an effect on community immediately after disturbance and later on. Thus, the drifting algal mats may be regarded as an efficient vector in spreading species (Norkko *et al.* 2000, Salovius *et al.* 2005, Arroyo *et al.* 2006) and they may contribute to the recovery of a benthic community after disturbance.

In terms of multivariate community measures, *i.e.* the dominance pattern of biomass distribution among species, the benthic community recovered within a vegetation period (**I**). 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 differed between control and disturbed plots. By autumn, there were no significant differences in phytobenthos variables due to the springtime disturbance. Contrarily, the total abundance and biomass of zoobenthos and the abundance of herbivores significantly differed between control and disturbed plots due to the springtime disturbance in autumn. This indicates that the species composition and the distribution pattern of abundance/biomass between species of zoobenthos recovered faster than the total abundance/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 springtime disturbance. The abundance and biomass of zoobenthos were higher in autumn compared to summer, which possibly explains the appearance of the effect of springtime disturbance in autumn but not in summer.

The springtime disturbance significantly reduced the number of phytobenthos species in summer (**I**). It decreased the biomass of both vascular plants and green algae. In addition to the direct effect of the disturbance, the removal of vascular plants, which provide a secondary substratum for epiphytes, contributed to a reduction of phytobenthos species richness and to a decrease in the biomass of green algae. Macrophytes are known to host a high diversity and density of epiphytes in the Baltic Sea (Wikström & 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 & 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 on 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 than zoobenthos (**I**). 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 (Nordström *et al.* 2009). The 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 & Orav 2001, Orav-Kotta & Kotta 2004, Salovius & Kraufvelin 2004).

Charophytes were the only group of plants that tended to be facilitated by a disturbance in spring (**I**). At the summer sampling, the charophyte biomass was higher on the disturbed plots than on the control plots. This pattern may be related to the timing of the disturbance, the seasonal succession of the phytobenthic community, and the competition between macrophytes. *Potamogeton pectinatus* is known to be competitively superior over charophytes (Van den Berg *et al.* 1998). The springtime disturbance took place before the seasonal appearance of charophytes and removed *P. pectinatus* therefore giving an advantage for the growth of charophytes. 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.

Unlike the sediment removal (**I**), the **sediment addition to the eelgrass *Zostera marina* meadow (II)** did not cause shifts in the community structure of zoo- and phytobenthos. The sediment addition did not cause statistically significant changes in the biomass of *Z. marina* either. Mills & Fonseca (2003) found that burial with 4 cm of sediment, which corresponded to 25 % of the average aboveground height (16 cm) of *Z. marina*, caused more than 50 % mortality of eelgrass. In the current study, only 2 cm of sediment, corresponding to less than 10 % of the height of eelgrass, was added. In addition to the relatively thin layer of added sediment, the lack of significant effects might be attributed to the naturally strong wave disturbance in the study area, *i.e.* the seagrass community is most likely adapted to high sediment mobility.

Seagrasses are known to 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 experiment (**II**) showed that the eelgrass (*Z. marina*) canopy significantly promoted the benthic species diversity and increased the 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, Boström & Bonsdorff 2000, Turner *et al.* 1999, Alfaro 2006). **The removal of eelgrass** significantly decreased the abundance and biomass of *Hydrobia ulvae*, *Corophium volutator*, *Idotea balthica* (Pallas), *Gammarus* spp., and *Cerastoderma glaucum* and the abundance of *Mytilus trossulus* and *Cerastoderma glaucum*. The removal of eelgrass decreased the biomass of all phytobenthic species but none of these differences was statistically significant. The canopy removal significantly decreased the total abundance and species richness of zoobenthos and the total biomass and species richness of phytobenthos. The losses due to the removal of the 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 the eelgrass canopy reduces the biomass of macroalgae and, consequently, causes a decrease in the density of herbivores such as gammarid amphipods and *Idotea balthica*. The removal of the eelgrass canopy significantly decreased the abundance of *Mytilus trossulus* in the present study. Eelgrass is known to facilitate the settlement of mussel larvae but also to provide a stable habitat for adults (Reusch & Chapman 1995, Bologna *et al.* 2005). The removal of the eelgrass canopy also decreased the densities of infaunal deposit feeders *Hediste diversicolor* and *Corophium volutator* which can be attributed to the reduced sedimentation rate of suspended matter and algal debris.

No interactive effects of the sediment addition and removal of the eelgrass canopy on the structure of the benthic community were found (**II**). However, interactive effects may appear if the intensity of physical disturbance is higher.

The addition of sediment did not cause changes in the organic matter content of the sediment of the experimental plots (**II**). As the sediment oxygen demand depends on its organic matter content (Terrados *et al.* 1999), the addition of sediment did not change the oxygen flux between the sediment and the water column (**II**).

Differently from the sediment addition, the eelgrass canopy had moderate effects on sediment properties (**II**). Eelgrass reduced the oxygen consumption of sediment in one sampling occasion out of four. No other statistically significant differences in the oxygen flux at the sediment-water interface due to eelgrass were found. During the third sampling higher seawater temperatures were measured compared to the other sampling periods and this may explain the significant differences in oxygen demand. The relatively low contribution of eelgrass to the oxygen flux complies with previous results of Pedersen *et al.* (1998) and Frederiksen & Glud (2006) who found that *Cymodocea rotundata* Ehr. ex Hemprich contributed only 1 % and *Zostera marina* 12 % of the total oxygen flux.

Similarly to the oxygen flux, the eelgrass canopy had a moderate effect on the content of organic matter in sediment (**II**). The content of organic matter was higher on plots with an eelgrass canopy than on plots where the canopy had been removed. A similar facilitative effect of seagrass on sedimentation of organic material was documented earlier for different seagrass species (Agawin & Duarte 2002, Peterson *et al.* 2004, Hendriks *et al.* 2008). Eelgrass significantly increased the sedimentation of fine particles (grain size < 100 µm). This result was in accordance with the findings in 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.

**Wave exposure** significantly affected the biomass and abundance structure of the recolonising benthic animals but did not affect the biomass structure of macrophytes in the short-term experiment (**III**). The total number of recolonising animal species was significantly higher in the sheltered site than the exposed site. This is in accordance with earlier observations that exposed areas with high sediment mobility are an inhospitable habitat for biota compared to sheltered areas hosting diverse benthic invertebrate communities (Gray 2002). Differences in the abundance structure of invertebrates due to exposure were mainly related to the higher abundance of *Cerastoderma glaucum* and Chironomidae larvae in the exposed site and the higher abundance of *Gammarus* spp. juveniles in the sheltered site. Differences in the biomass structure of invertebrates due to exposure were mainly related to the higher biomass of *Saduria entomon* (L.) in the exposed site and the higher biomass of *Cerastoderma glaucum* and *Hydrobia ulvae* in the sheltered site. The total invertebrate biomass was higher in the sheltered site than in the exposed site.

In the long-term experiment (**IV**) wave exposure had significant effects on herbivores at the later stages of annual succession in July–August. Similarly to the short-term experiment, the biomass of gammarid amphipods was significantly higher in the sheltered area than in the exposed area, when the community was dominated by juvenile amphipods in July. However, when the community was dominated by adult amphipods in August, the opposite was found. Contrarily to the short-term experiment, exposure significantly affected macrophyte communities in the long-term experiment. Exposed areas were characterised by higher biomasses of *Ulva intestinalis* L., *Pilayella littoralis*

(L.) Kjellm. and *Chara aspera* than sheltered areas. These results suggest that many macrophytes, including fragile charophytes, benefit from a moderate wave exposure. This may be explained by the lower sedimentation load, lack of drifting algae, and better light regimes in more exposed areas. Among benthic invertebrates, however, only those can benefit from an elevated exposure that can find shelter and food among macrophytes.

**The initial invertebrate community (III)**, which consisted of all possible combinations of the suspension feeder *Cerastoderma glaucum*, the deposit feeder *Macoma balthica*, and the herbivore *Theodoxus fluviatilis* on soft bottoms, had no effect on the mortality of seeded animals and on the abundance and biomass structure of colonised invertebrate and macrophyte communities. This indicates that colonisation is driven mainly by physical factors. Many species-poor ecosystems are dominated by resource generalists, and the addition of new species may add no new function (Parker *et al*. 2001). Both *M. balthica* and *C. glaucum* can potentially switch between suspension and deposit feeding modes (Brafield & Newell 1961, Ólafsson 1986, Hawkins *et al*. 1990, Kang *et al*. 1999, Herman *et al*. 2000), which may partly explain the paucity of biotic interactions in this study. Besides, the duration of the experiment might have been too short for the biotic interactions to come into play.

However, in the other mesocosm experiment on both soft and hard bottoms (**IV**) the presence of the **suspension feeding mussel *Mytilus trossulus*** had a significant effect on the benthic community. This suggests that *M. trossulus* is a more influential habitat modifying species compared to *C. glaucum*, *M. balthica*, and *T. fluviatilis*. The effect of the mussel was related to the increased biomass of ephemeral filamentous algae, herbivores, and deposit feeders and the decreased biomass of charophytes. The mussel *M. trossulus* facilitated the growth of filamentous algae indicating that faeces and pseudofaeces of mussels provide a nutrient source for macroalgae. The addition of nutrients may be either direct (through nitrogenous excretory products) or indirect (through biodeposition and subsequent mineralisation) (Kautsky & Wallentinus 1980, Dame *et al*. 1991, Bracken & Nielsen 2004). The facilitative effect of mussels on filamentous algae appeared only at the beginning of the seasonal succession of macrophytes (June, July), although it is possible that *M. trossulus* facilitates the growth of algae throughout the productive season. However, the grazing pressure by herbivores is heavier at the later stages of macroalgal succession, possibly counteracting the facilitative effect of mussels. Treatments with *M. trossulus* had significantly higher biomasses of herbivores in August and September than treatments without the mussel.

The interaction of exposure and *M. trossulus* had an effect on the biomass of filamentous algae (**IV**). The facilitative effect of *M. trossulus* on filamentous algae was stronger in the moderately exposed area compared to the sheltered area. This pattern may indicate that mussels had poorer food supplies in the sheltered site than in the moderately exposed site, resulting in their lower biodeposition and weaker effect on algae in the former site.

Numerous studies have shown that higher macroalgal biomass supports higher densities of herbivores as plants provide herbivores with habitat and food resources (Huntly 1991, Lawton 1994, Kotta & Orav 2001, Orav-Kotta & Kotta 2004). A positive effect of mussels on herbivores was found in July to August (**IV**). This pattern can be explained by the facilitative effect of *M. trossulus* on filamentous algae, which in turn support higher densities of herbivores. The mussel enhanced the growth of the filamentous brown alga *Pilayella littoralis*, which is the preferred food item for the prevalent herbivores – the gammarid amphipods (Orav-Kotta *et al.* 2009).

Besides herbivores, *M. trossulus* facilitated also deposit feeders (**IV**). This result supports the previous findings that accumulation of faecal material of mussels induces increased settlement and densities of deposit feeders (Posey 1986, Dittmann 1990, Snelgrove & Butman 1994). The positive effect of mussels on deposit feeders was observed in the early stages of annual benthic succession. Drifting algal mats and their decomposition products provide deposit feeders an additional source of food in the later stages of annual succession (Lauringson & Kotta 2006) and this may explain the weak effects of mussels in this period.

**Large-scale dredging (V)** in Muuga Bay had weak but consistent effects on benthic invertebrate communities and the recovery of the communities took place within a year. This supports the hypothesis that stress-tolerant species of the Baltic Sea can easily cope with dredging activities. Communities that are characterised by opportunistic species often show weak effects of and fast recoveries from dredging (Gorzelany & Nelson 1987, Bolam & Rees 2003, Robinson *et al.* 2005). Hinchey *et al.* (2006) and Powilleit *et al.* (2006) also demonstrated that *M. balthica* dominated communities are weakly affected by the disposal of dredged material and communities recover within a short period of time. On the other hand, Olenin (1992) demonstrated that several common benthic invertebrate species of the Baltic Sea are sensitive to dredging; however, the effects are significant for species abundances only and not for biomasses. Weak impacts and a high recovery potential of benthic communities are supported by a relatively high exposure of the study area (Newell *et al.* 1998). The study area has a good water exchange with the deeper sea and hypoxic conditions are not likely in Muuga Bay. A rapid recovery is also expected due to a very strong seasonality of the Baltic Sea, strong natural physical disturbance, and short generation times of most near-coastal animal species (Hällfors *et al.* 1981). The effects of dredging were mainly manifested as changes in the biomass of bivalves, especially in that of *M. balthica*. The biomass increased manifold during the year of dredging, especially at those areas that had lower water exchange, *i.e.* on flat bottoms. This could be expected as flat bottoms are characterised by lower water exchange than slopes. With increasing water exchange the amount of deposited organic matter, *i.e.* food of benthic invertebrates, decreases (Newell *et al.* 1998).

# 4. CONCLUSIONS

To conclude, physical disturbance and habitat-modifying species had manifold separate and interactive effects on sediment properties and benthic communities:

- The disturbance involving the removal of the upper layer of seabed sediment had no effect on the sediment organic matter content but decreased species richness and densities of benthic species. The effect of the disturbance was stronger in spring than in summer. In summer, drifting algal mats quickly carried most of the local species to the disturbed patches. The species composition recovered faster than the densities of benthic invertebrates (**I**).
- Accumulation of a thin layer of sediment on the eelgrass (*Zostera marina*) meadow did not affect the content of sediment organic matter, the sediment oxygen flux, and the structure of the benthic community. Contrary to the addition of sediment, the removal of the canopy of eelgrass significantly decreased the sedimentation of fine particles, temporarily increased the sediment oxygen consumption, influenced the dominance structure of benthic community, and decreased the species diversity and species' densities (**II**).
- When communities were assembled from *Cerastoderma glaucum*, *Macoma balthica*, and *Theodoxus fluviatilis*, the dominance structure of the colonising invertebrates depended on the wave exposure rather than on the initial composition of the invertebrate community. This indicates that physical factors are more important drivers of invertebrate colonisation than the initial faunal composition in such communities (**III**). However, the suspension feeding bivalve *Mytilus trossulus* enhanced the growth of filamentous algae, herbivores, and deposit feeders and decreased the biomass of charophytes (**IV**). Stronger effects of *M. trossulus* emerged in the moderately exposed than in the sheltered area.
- Large-scale dredging had weak but consistent effects on benthic invertebrates both in space and time. The recovery of the communities took place within a year. The effects of dredging mainly appeared as an elevated biomass of bivalves, especially that of *Macoma balthica*. These bivalves were more impacted on flat bottoms than on steeper slopes (**V**).

# SUMMARY IN ESTONIAN

## Füüsikalise häiringu ja elupaika kujundavate liikide mõju põhjasette omadustele ja põhjakooslustele Läänemere põhjaosas

Häiringud on oluliseks looduslikke kooslusi kujundavaks teguriks põhjustades koosluste ruumilist ja ajalist muutlikkust. Häiringuid on defineeritud eelkõige kui ebakorrapäraselt toimuvaid sündmusi, mis kutsuvad esile muutusi ökosüsteemi, koosluse või populatsioonide struktuuris. Häiringud eemaldavad kooslustest organisme ning loovad vaba ruumi uutele tulijatele. Kuna nii häiringud kui ka vaba ruumi koloniseerimine on ajas ja ruumis üsna juhuslikud, siis toetavad mõõdukad häiringud bioloogilise mitmekesisuse tekkimist ja säilimist. Peamisteks füüsikalisteks häiringuteks mere sublitoraalis on lainetuse ja hoovuste kulutav toime, jää kraapiv toime, setete alla mattumine, ebaharilikult kõrge või madal vee temperatuur või soolsus ja hapnikupuudus. Lisaks looduslikele füüsikalistele häiringutele põhjustab ka inimtegevus, nagu näiteks laevandus, süvendamine ja kaadamine, ehitustööd meres, maavarade ammutamine ja kalapüük põhjatraaliga, füüsikalisi häiringuid mere põhjale. Viimaste aastakümnete kliimamuutustega on kaasnenud tormide intensiivsuse ja sageduse suurenemine, mistõttu füüsikaliste häiringute mõju ökosüsteemide kujunemisele üha suureneb.

Teatud liigid võivad kujundada elupaiga füüsikalist struktuuri ja aineringet. Sellised elupaika kujundavad liigid suurendavad elupaiga ruumilist mitmekesisust, muudavad keskkonnatingimusi ja suurendavad toidubaasi ning loovad seeläbi tingimusi suurema liigilise ja funktsionaalse mitmekesisusega koosluste tekkeks. Tüüpilisteks elupaika kujundavateks organismideks Läänemere põhjasosas on suurtaimestik ja karbid.

Nii häiringute kui ka elupaika kujundavate liikide mõju on uuritud eelkõige tõusu-mõõna vööndis. Vähe on teadmisi füüsikaliste häiringute ja koosluse võtmeliikide eraldi ja koosmõjust mere sublitoraali põhjaelustikule. Doktoritöö peamiseks eesmärgiks oligi uurida füüsikalise häiringu ja elupaika kujundavate liikide mõju põhjasette iseloomule ning põhjakooslustele Läänemere põhjaosas. Uurimuse raames teostati neli *in situ* manipulatiivset katset Liivi lahe põhjaosas ja Soome lahe lääneosas, mille käigus uuriti:

- merepõhja pealmise settekihi eemaldamise (tugeva tormi või jää kulutava mõju imiteerimine) ja selle toimumise aja (kevad, suvi) mõju põhjaelustikule ja sette orgaanilise materjali sisaldusele;
- sette akumuleerumise ja elupaika kujudava liigi (pikk merihein, *Zostera marina*) eraldi ja koosmõju põhjaelustikule ja -settele (orgaanilise materjali sisaldus, granulomeetriline koosseis, hapnikuvoog);
- põhjaloomastiku võtmeliikide ja lainetusele avatuse mõju põhjakoosluste arengule.

Lisaks uuriti pikaajaliste vaatlusandmete analüüsil ulatuslike süvendustööde mõju põhjaloomastikule.

Füüsikalise häiringu ja elupaika kujundavatel liikide mõju ja koosmõju põhjasette omadustele ja põhjakooslustele oli varieeruv. Olulisemad tulemused on järgnevad:

- Pealmise settekihi eemaldamine vähendas põhjaelustiku liigirikkust ja asustustihedust, kuid ei mõjutanud orgaanilise materjali sisaldust põhjasettes. Häiringu mõju oli tugevam kevadel. Suvel leidus katsepiirkonnas hulgaliselt lahtist vetikamatti, mis kandis häiringualadele suurema osa kohalikest põhjaelustiku liikidest. Põhjaloomastiku domineerimisstruktuur taastus kiiremini kui liikide asustustihedused.
- Õhukese settekihi akumuleerumine pika meriheina kooslusele ei põhjustanud muutusi põhjasette orgaanilise materjali sisalduses, sette ja veesamba vahelises hapnikuvoos ja põhjaelustiku struktuuris. Küll aga mõjutas põhjaelustikku meriheina eemaldamine, mille tagajärjel langes oluliselt liigirikkus ja põhjaorganismide asustustihedus. Meriheina eemaldamine vähendas ka peeneteralise fraktsiooni hulka settes ja suurendas ajutiselt sette hapnikutarvet. Seega oli elupaika kujundava liigi mõju tugevam kui füüsikalise häiringu mõju.
- Katses, kus esialgne põhjaloomastiku liigiline koosseis komplekteeriti söödavast südakarbist (*Cerastoderma glaucum*), balti lamekarbist (*Macoma balthica*) ja vesikingast (*Theodoxus fluviatilis*), ei sõltunud koloniseeriva põhjaloomastiku koosluse domineerimisstruktuur esialgsest liigilisest koosseisust vaid avatusest lainetusele. See näitab, et koloniseerimise algfaasi mõjutavad rohkem abiootilised keskkonnategurid kui biootilised seosed.
- Söödav rannakarp (*Mytilus trossulus*) suurendas niitjate vetikate, herbivooride ja detrivooride hulka kuid vähendas mändvetikate biomassi. Rannakarbi mõju oli suurem lainetusele mõõdukalt avatud piirkonnas võrreldes lainetuse eest varjatud piirkonnaga.
- Ulatuslike süvendustööde mõju põhjaloomastikule oli nõrk ja koosluste taastumine oli kiire. Mõju väljendus peamiselt karpide, eriti balti lamekarbi, biomassi suurenemises. See näitab, et kõrge stressitaluvusega Läänemere põhjaloomastiku liigid elavad kergesti üle süvendustöödega seotud häiringud.

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# PUBLICATIONS

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**Scientific publications:**

Herkül K., Kotta J. & Pärnoja M. Effect of physical disturbance on the soft sediment benthic macrophyte and invertebrate community in the northern Baltic Sea. Boreal Environ. Res., 16 (in press).

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