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Distribution, feeding and habitat
of benthic suspension feeders
in a shallow coastal sea



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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers referred to in the text by their Roman numerals:

- I. Oganjan K., Lauringson V., 2014. Grazing rate of zebra mussel in a shallow eutrophicated bay of the Baltic Sea. *Marine Environmental Research*, 102, 43–50.
- II. Kotta J., Oganjan K., Lauringson V., Pärnoja M., Kaasik A., Rohtla L., Kotta I., Orav-Kotta H., 2015. Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. *PLoS One*, 10 (8), e0136949, journal.pone.0136949.
- III. Oganjan K., Lauringson V., Kotta J., Rostin L., Martin G., 2017. Factors affecting the recruitment of *Amphibalanus improvisus* and *Dreissena polymorpha* in a highly eutrophic brackish bay. *Estuarine, Coastal and Shelf Science*, 184, 37–45.
- IV. Torn K., Herkül K., Martin G., Oganjan K., 2017. Assessment of quality of three marine benthic habitat types in NE Baltic Sea. *Ecological Indicators*, 73, 772–783.

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AUTHOR'S CONTRIBUTIONS

- | | |
|-----------|--|
| Paper I | – Contributed to the design and planning of the study, participated in the field work, performed the experiments, analysed samples in the lab, performed data statistical analyses, responsible for writing the manuscript |
| Paper II | – Contributed to the design of the paper, contributed to the data statistical analyses, participated in the manuscript writing and finalization |
| Paper III | – Participated in the design and planning of the study, participated in the field work, analysed samples in the lab, performed data statistical analyses, wrote the manuscript |
| Paper IV | – Contributed to the design and planning of the study, participated in the collection of data, analysed samples in the lab, contributed to data compilation, participated in the manuscript drafting and finalization |

LIST OF ABBREVIATIONS

BRT	Boosted Regression Trees
BSF	Benthic suspension feeders
EH	External horizontal surfaces
EV	External vertical surfaces
HD	The Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora)
HID	Internal horizontal downwards orientated surfaces
HIU	Internal horizontal upwards orientated surfaces
IV	Internal vertical surfaces
SPM	Suspended particulate matter
SPIM	Suspended particulate inorganic matter
SPOM	Suspended particulate organic matter
TSS	Total suspended solids

1. INTRODUCTION

Marine ecosystems provide a broad range of ecological, scientific and socio-economic services critical for human welfare. Since climate change presents new challenges for marine ecosystems, understanding how environmental factors drive species ecology has created a new sense of urgency. Knowledge of marine species growth, survival, distribution and abundance is of major importance for the efficient management of marine resources.

Marine organisms have adapted to a multitude of niches and exhibit extremely diverse behaviours. Coastal environments are often dominated by sessile species that attach to marine substrates to live a relatively sedentary life. The existence of such sessile epibenthic communities is controlled by an array of ambient processes: choice of settling sites, recruitment of larvae, and biotic and abiotic events (Grosberg, 1981).

Three types of **environmental gradients** are recognised as major forces in structuring sessile communities during and after settlement: direct gradients, indirect gradients and resources (Austin, 1980). Direct environmental gradients have a physiological influence on species but are not consumed, e.g. temperature and salinity. Indirect environmental gradients do not themselves have a direct physiological influence but represent proxies for a set of other underlying direct gradients, e.g. water depth is a typical indirect variable in the aquatic systems. Finally, resources are directly consumed by organisms, e.g. nutrients. Moreover, it is often difficult to distinguish between the above-mentioned types of gradients when the same factor acts via different pathways. For example, water movement can: (a) directly physically detach sessile organisms, (b) indirectly modify sedimentation rates, or (c) alter resource supply (Austin, 1980; Austin and Smith, 1989).

In addition to environmental factors, **biotic interactions** with ambient organisms other than resources play a major role in structuring communities (Menge and Sutherland, 1987). Space, i.e. available substrate to attach to, is often one of the most important limiting resources for the settlement, growth and survival of sessile communities, causing competition (Schoener, 1983; Bertness and Leonard, 1997). Habitat segregation between potentially competing species may offer a way to relieve competition in the use of spatial resources allowing them to coexist. Depending on the magnitude of a particular structuring component, habitat selection may be a response to ongoing competition between species or an outcome of environmental filtering (Rosenzweig, 1981; Brown and Rosenzweig, 1986).

When environmental conditions are severe, disturbances will structure populations. Such disturbances may be physical (dislodgment by wave action, abrasion by currents, ice scour, burial in the sediment) or physiological (temperature, salinity, hypoxia conditions). Regardless of its origin, disturbances clear space that supports co-existence of species. In moderate environmental conditions the role of competition increases as stress decreases, while further

stress reduction results in increased predation and reduction in competition (Tilman 1994; Menge & Sutherland 1987). If such disturbances are absent, interspecific competition intensifies and only a restricted number of species can occupy the limiting resource (Dayton, 1971; Menge, 1976; Sousa, 1984).

As a rule, benthic invertebrate communities in the **Baltic Sea** are regulated by abiotic environmental factors rather than biotic interactions (Kautsky 1981; Eriksson & Bergström 2005; Wallin et al. 2011). That said, the Baltic Sea still represents a stressful habitat for organisms, with many living on the edge of their physiological tolerance limits. The Baltic Sea ecosystem is under pressure from natural gradients in salinity and seasonal temperature fluctuations, hypoxia in deeper areas, strong storm events and winter-time ice scour (Voipio, 1981; Meier et al., 2012). Salinity is considered to be one of the most important factors regulating the distribution of species in the Baltic Sea (Gogina and Zettler, 2010). Brackish conditions cause physiological stress that manifests in the decreased body size and slower growth rate of many Baltic Sea species (Tedengren and Kautsky, 1986). Species diversity decreases dramatically along the salinity gradient which steadily declines towards north and east. Low salinity is responsible for the low functional diversity in the northern Baltic Sea where one functional group is often represented by a few or a single species that essentially uphold important ecosystem functions (Kiirikki, 1996; Rumohr et al., 1996; Bonsdorff, 2006).

On top of natural stress, multiple **human activities** place heavy pressures on the Baltic Sea ecosystem. Among anthropogenic pressures, introduction of non-indigenous species and eutrophication of the coastal waters are considerable problems in the Baltic Sea, especially in shallow, inshore areas (Helsinki Commission, 2009). In addition, climate change is expected to alter marine ecosystems, making them even more vulnerable to cumulative pressures. Model simulations of potential future climates in the Baltic Sea region predict increases in temperature and precipitation with accompanying changes, such as increase in freshwater input, intensity of cyclonic activity and frequent winter storms, as well as decreases in salinity, ice cover and seawater pH (Andersson et al., 2015; Vuorinen et al., 2015). Effects of climate change are expected to favour invasive species (Dukes and Mooney, 1999; Holopainen et al., 2016), opening up new ecological niches for biological invasions and causing additional pressures on the Baltic species and habitats already living under stressful conditions.

Moderate eutrophication has promoted **benthic suspension feeders (BSF)**, which grow amply due to an increase in their food supply. Benthic suspension feeders are widespread along the coast of the Baltic Sea owing to a lack of their main invertebrate predators in brackish-water conditions. Being relatively immobile, BSF depend on the particle flux in the movement of water to introduce food to their habitats (Okamura, 1990). On the one hand, they depend on resource availability. On the other hand, they can control phytoplankton by the top-down mechanisms through their grazing ability and deliver nutrients from the pelagic to the benthic system. They thus directly regulate pelagic primary

production and indirectly secondary production (Gili and Coma, 1998). At high abundances, certain BSF can act as ecosystem engineers, and influence species richness and composition of benthic communities by increasing habitat complexity, acting as additional substrate for attachment, protecting from predation, competition and environmental stresses, and serving as a food resource (Eckman and Duggins, 1991; Dame et al., 2001). In recent years, BSF have received particular attention because of the role that they play in eutrophicated waterbodies (Reeders and Bij de Vaate, 1990; Lindahl et al., 2005; Stybel et al., 2009). BSF are considered a natural eutrophication control, especially in shallow, turbid, nutrient replete systems (Officer et al., 1982). They function as natural biological filters and remove large amounts of suspended particles from the water column, acting as a sink for nutrients and organic matter (Dame and Olenin, 2005).

Invasive suspension feeders have been particularly successful in shallow eutrophic estuarine conditions of the Baltic Sea (Olenin and Leppäkoski, 1999; Leppäkoski and Olenin, 2000; Zaiko et al., 2010). First of all, high pelagic production due to eutrophication in the coastal areas and active use of anthropogenic vectors facilitate the invasion of suspension-feeders (Olenin and Daunys, 2005). Next, their effective feeding adaptation is believed to make them optimal foragers in aquatic environments owing to low levels of energy cost of active filtering (Gili and Coma, 1998). This adds up to other characteristics that influence invasion success such as ecological plasticity, effective reproduction, dispersal strategy, and high flexibility in substrate choice, making them outstanding colonisers of new environments (Gili and Coma, 1998; Ruiz and Hewitt, 2002; Olenin and Daunys, 2005).

The most prominent **epibenthic suspension-feeders in the Baltic Sea** are mussels of the *Mytilus edulis* complex (hybrids of *Mytilus edulis* x *Mytilus trossulus*) and *Dreissena polymorpha* Pallas, and the cirriped *Amphibalanus improvisus* Darwin (Bonsdorff and Pearson, 1999; Bonsdorff, 2006). More saline parts of the Baltic Sea are inhabited by the native mussels *M. edulis* (blue mussel), *M. trossulus* (bay mussel), and the non-indigenous North American cirriped *A. improvisus* (bay barnacle), which are amongst the most common benthic invertebrate species in the Baltic Sea (Helsinki Commission, 2012). Oligohaline parts of the Baltic Sea are populated by non-indigenous *A. improvisus* and the Ponto-Caspian bivalve *D. polymorpha* (zebra mussel) (Olenin and Leppäkoski, 1999; Bonsdorff, 2006). Both indigenous and non-indigenous species are sensitive to climate change, which can be expected to induce shifts in distribution limits of these species. While some species will probably expand their distribution range, others will retreat (Wikström and Kautsky, 2007; Vuorinen et al., 2015; Holopainen et al., 2016).

The role of suspension-feeder species in coastal ecosystems as functional and habitat modifiers is an established ecological concept and justifies their **protection and conservation** (Gili and Coma, 1998; Dame et al., 2001; Norling and Kautsky, 2008). The progress in protecting marine sites has been much slower than on land and many gaps still remain (European Commission, 2015a).

Although motivation for conservation is similar between terrestrial and marine systems, they require distinct approaches due to differences in ecosystem processes and in human perceptions (Carr et al., 2003). Firstly, conservation of the marine environment has been complicated due to expensive fieldwork and lack of information available on distribution and abundance of different marine species and habitats. According to the latest reports, knowledge of marine habitats and species remains poor and their monitoring requires a significant additional effort (European Commission, 2015). Secondly, there is a broad range of cumulative pressures on the marine environment from different sectors, which makes individual objectives difficult to achieve (Fulton et al., 2015). However, advancements in research in the fields of basic biology, physiology and ecology are increasingly being integrated with applied conservation such as habitats monitoring and quality assessment (Lundquist and Granek, 2005; Cvitanovic et al., 2015).

Because of their role in coastal ecosystems, BSFs have received legal consideration, as reflected in the EU Habitats Directive (EEC/92/43) (HD), which aims to conserve natural habitats and species within them. In the framework of the HD, *A. improvisus*, *D. polymorpha* and *M. trossulus* are crucial to the ‘reefs’ habitat type (habitat type code 1170), acting there as reef forming species. ‘Reefs’ are a marine habitat of conservation importance and protection under Annex I of the HD (Paal, 2007). Habitat is of great conservation value due to the structuring role it plays in the areas with higher hydrodynamic activity and the complex environment that it provides for benthic species (Paal, 2007; European Commission, 2013).

Despite a growing number of field and experimental works, many **knowledge gaps** persist on how various biotic and abiotic gradients shape feeding behaviour, distribution patterns and coexistence of BSF species in the native range as well as invaded ecosystems. **Firstly**, we lack understanding on how non-indigenous species interact with each other in their invaded range. Regardless of their ubiquity, *in situ* research on coexistence of *A. improvisus* and *D. polymorpha* is missing. There are studies on the biological interactions between non-indigenous barnacles and native mussels of the *Mytilus* complex (Järvekülg, 1979; Dürr and Wahl, 2004), but no studies on biological interactions between non-indigenous zebra mussels and barnacles. **Secondly**, environmental requirements for zebra mussel feeding are poorly understood. Feeding has been estimated using different methods, complicating comparison between studies (Dionisio Pires et al., 2004; Naddafi et al., 2007; Zaiko and Daunys, 2011). *In situ* studies about effects of different environmental variables to *D. polymorpha* feeding in the Baltic Sea are scarce (Kotta and Mohlenberg, 2002; Lauringson et al., 2014). Since zebra mussels can be a valuable tool in the eutrophication control, it is important to understand potential obstacles as well as conditions favouring their settlement, coexistence with other species, and feeding. **Thirdly**, most information on the distribution of *Mytilus* comes from intertidal communities (Menge et al., 1997; Commito and Dankers, 2001). However, non-tidal communities are structured by different mechanisms. Patterns of

M. trossulus distribution and biomass along different environmental gradients in the north-eastern Baltic Sea remain poorly studied. **Finally**, there is no published information available concerning the quality assessment of benthic habitats in the Baltic Sea or neighbouring areas (Louette et al., 2015). In relation to conservation, most studies have explored the main threats affecting species and habitats. However, planning relevant conservation actions needs information on the quality of the habitats. Quality assessment should be based on a set of scientifically sound habitat-specific criteria and their reference values. Habitat quality assessment requires knowledge on what types of criteria are appropriate for particular types of habitat, the natural range of variation for different habitat types and species, and how local habitat structure will respond to critical changes and disturbances.

There are several reasons for these knowledge gaps. To begin with, numerous factors and interactions between these factors potentially influence benthic suspension feeders, e.g. benthic–pelagic links, water movement, physical disturbances, and biological interactions (Underwood, 1985; Nyström-Sandman et al., 2013). Further, complexity in system dynamics results in high variability in direction and magnitude of responses among different ecosystems (Menge and Branch, 2001; Witman and Dayton, 2001). Generalised results help to grasp the significance of the processes on a larger scale; however, they are too coarse for local assessment. Detailed knowledge on the ecology of syntopic species is highly important for conservation and human pressure mitigation, as numerous species with complementary traits will be required to buffer the impact of cumulative pressures on important ecosystem functions. Therefore, continuous and progressive evaluation of suspension feeders' distribution and feeding behaviour is necessary to predict spatial and temporal patterns of their growth, and their effect on surrounding communities under changing climate. This helps further comprehend ecosystem functioning, protect marine resources and retain ecosystem integrity.

1.1. Objectives

The general aim of this thesis was to describe feeding (I), distribution (II–III), and coexistence (III) of benthic suspension-feeders, and assess their habitat quality (IV) in the north-eastern Baltic Sea. The specific objectives were to:

- Examine the feeding behaviour of the wild population of a non-indigenous species *D. polymorpha* in relationship with multiple environmental factors in eutrophic conditions (I). Feeding rates of mussels were derived from field populations by measuring the content of algal pigments in specimens collected from their natural habitat. The content of pigments was converted to feeding rate using field experiments measuring the loss of chlorophyll-*a* during gut passage and biodeposition of mussels.
- Describe the realised niche of the mussel *M. trossulus* in the north-eastern Baltic Sea, both in terms of distribution and the size of populations (II). We examined the role of direct environmental and resource gradients in describing the distribution and standing stock of *M. trossulus* using existing data derived from the database of the Estonian Marine Institute and environmental niche modelling.
- Examine the colonization and coexistence of *A. improvisus* and *D. polymorpha* in their invaded range in response to environmental forcing in eutrophic conditions (III). Artificial substrate was used as a standardised hard substrate to estimate colonization and microhabitat use of these two species along different environmental gradients in a highly eutrophic bay.
- Apply collected scientific data on the abundance and biomass of species to assess habitats' quality in the Estonian sea (IV). The assessment criteria and favourable reference values were determined using existing data derived from the database of the Estonian Marine Institute.

2. MATERIALS AND METHODS

2.1. Study species

Hard-bottom suspension-feeder communities in the northern Baltic are dominated by three highly gregarious species, which are studied in the present thesis: *Amphibalanus improvisus* Darwin, *Dreissena polymorpha* Pallas and *Mytilus trossulus* Gould (Figure 1).

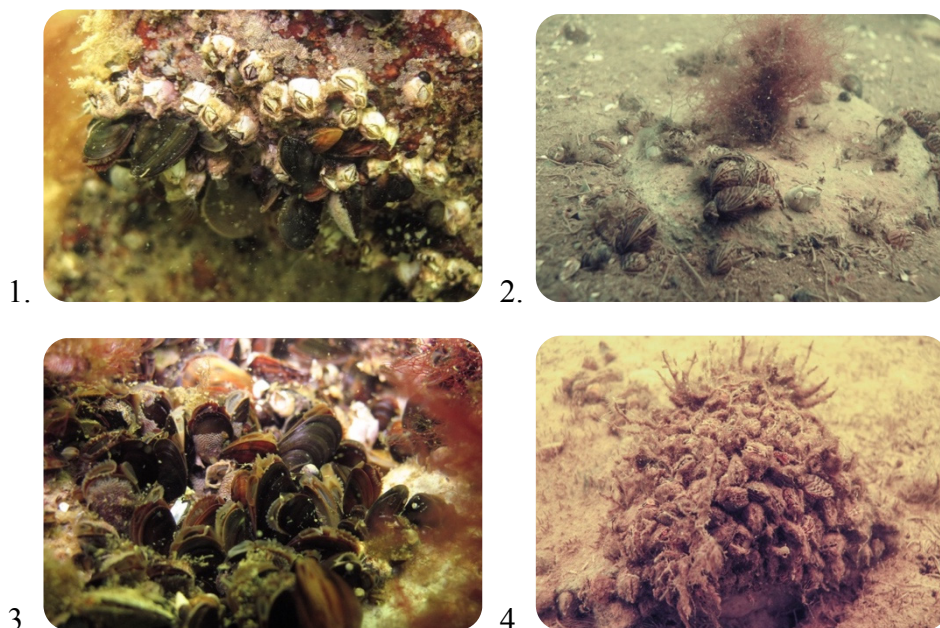


Figure 1. Photographs of the study species: (1) *A. improvisus* and *M. trossulus*, (2) *A. improvisus* and *D. polymorpha*, (3) *M. trossulus*, (4) *D. polymorpha*. Photos by Kaire Kaljurand.

Bay barnacle *A. improvisus* (III–IV) is an invasive suspension-feeding crustacean from North America, which was introduced to the Baltic Sea in the late 19th century. It occurs in mesohaline environments and can survive in fresh water. *A. improvisus* has a high reproductive and fouling capacity and is usually among the first macro-colonisers of the hard-bottom communities. It uses almost any available hard surface as a substratum, such as rocks, bivalve shells, macroalgae, and artificial hard surfaces. *A. improvisus* is the only barnacle species living in the coastal waters of the Baltic Sea. It dominates over large areas and is the most widespread fouling organism in the Baltic Sea but it does not have a negative effect on community diversity in the Baltic (Dürr and Wahl, 2004). *A. improvisus* is abundant in eutrophicated bays where its abundance can be considerably greater compared to natural environments. *A. improvisus* is subdominant to *M. trossulus*, which is a stronger competitor for space and both

species together are capable of outcompeting other epifaunal species for space occupancy (Järvekülg, 1979; Dürr and Wahl, 2004).

Zebra mussel *D. polymorpha* (I, III, IV) is an invasive suspension-feeding bivalve first introduced to the Baltic Sea in the 19th century, probably by ballast water and hull fouling of vessels from the Ponto-Caspian region. Since then, it has established abundant populations in several oligohaline bays and estuaries, except for the northern part of the basin where lower temperatures limit the species. Their distribution in the Baltic Sea is patchy, as mussels require suitable habitat for attachment. Mussels dominate stony and mixed bottoms. They can also colonise sedimentary habitats using their byssal threads to bind sediments in conglomerates and form clumps. Settlement is possible on a large variety of substrates, contributing to their successful introduction and possible invasion in new habitats. *D. polymorpha* prefers moderately productive mesotrophic water bodies. *D. polymorpha* may, in favourable conditions, form large aggregations. *D. polymorpha* may co-occur with *A. improvisus* and *M. trossulus* and dominates the latter in more diluted areas (Karatayev et al., 1997; Ward and Ricciardi, 2007).

Bay mussel *M. trossulus* (II, IV) is a common benthic suspension feeder in the temperate zone of the northern hemisphere, which inhabits both subtidal as well as intertidal areas. *M. trossulus* is one of the three principal, closely related taxa in the *Mytilus edulis* complex of blue mussels, which can hybridise with each other if present at the same locality. *M. trossulus* tolerates a wide range of environmental conditions and can gain high biomass at different habitat types. In the brackish non-tidal Baltic Sea, *M. trossulus* is an important organism in various hard- and mixed-bottom subtidal habitats. In the Baltic Sea, *M. trossulus* coexists with *M. edulis*. Here, all mytilids are hybrids, with varying fractions of *M. edulis* alleles in their genomes. As a key ecological differentiation, *M. trossulus* tolerates lower salinity compared to *M. edulis* and thereby populates almost the whole range of the Baltic Sea. The species inhabits hard-bottom substrate like rocky bottoms, gravel, boulders and cobbles, as well as soft bottoms forming clumps or attaching to benthic vegetation. In the Baltic Sea, salinity is regarded as the ultimate abiotic factor regulating the distribution of *M. trossulus*. Low salinity is also responsible for the decreased body size and slower growth rate of the species (Kautsky and Evans, 1987; Väinölä and Hvilsum, 1991; Westerbom et al., 2002; Stuckas et al., 2009).

2.2. Study area

The studies for this thesis were carried out in the Pärnu Bay (I, III) and along the Estonian coastal area (II, IV) located in the north-eastern Baltic Sea (Figure 2). The Estonian coastal area includes parts of the Gulf of Finland, the Gulf of Riga, the whole West Estonian Archipelago Sea and part of the Baltic proper. Salinity in the Estonian waters is constantly low, varying between 2 to 8 in the surface layers, whilst major parts of the area have salinity around 6. The area is

characterised by the absence of tides, although very shallow areas are sporadically exposed by wind action. Wave energy is low as compared to the coasts of the large oceans, but may still be significant for the bottom organisms at shallow exposed sites, particularly during autumn and winter storms. Shallow areas may be subjected to intense wintertime ice scour. The area embraces major geomorphological structures including different types of soft bottoms, limestone and granite bedrock. Freshwater and terrestrial runoff influence the areas around major river inlets. Shallow depths prevail in the western part of the study area while the southern part of the Gulf of Finland has a relatively steep coastal slope (Feistel et al., 2008; Leppäranta and Myrberg, 2009).

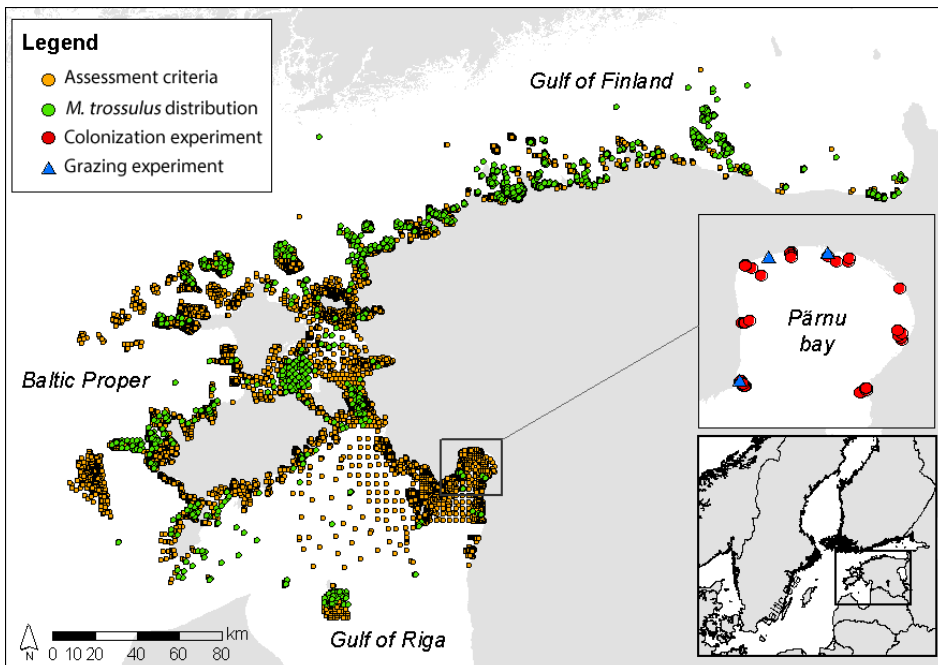


Figure 2. Study area and sampling locations

Pärnu Bay, situated in the Gulf of Riga, is an excellent non-tidal model system: (a) due to intensive water mixing in this shallow water ecosystem, water chlorophyll-*a* is a good proxy for the food supply of BSF; (b) two non-indigenous BSF species occur syntopically in this area. It is a shallow sheltered bay with high spatial and temporal gradients in temperature and salinity. The bay is strongly influenced by the inflow of the Pärnu river and suffers from heavy anthropogenic eutrophication due to riverine loads. The salinity in the bay is 3–6. The currents are generally weak and are predominantly wind induced. The bottom relief is quite flat, with gentle slopes towards deeper areas. Prevailing bottom sediments are soft, varying from sand to silty clay or mud; these are inhabited by soft-bottom fauna. There are also patchy areas of mixed sediments that are inhabited by zebra mussels, and bay barnacles attached to

small stones and pebbles. Maximum depth is 8 metres. Poor water transparency due to wind-induced resuspension of clayish sediments and high contents of riverine plume are coupled with the lack of macrovegetation. The phytobenthic community is poorly developed. Macrozoobenthos is characterised by low species diversity, moderate overall abundance and biomass, and the prevalence of 1–2 dominant species (Kotta et al., 2008). Biomass of benthic invertebrates is dominated by the non-indigenous species *A. improvisus* and *D. polymorpha*.

2.3. Data collection

2.3.1. Experimental designs

This chapter briefly describes the methods used to fulfil the aims of the present thesis. Detailed descriptions of the methods are provided in the relevant papers.

Grazing rates of *D. polymorpha* (I) were studied by experiments conducted in the Pärnu Bay, Gulf of Riga. *In situ* incubations were carried out at three locations from April to December 2012 (Figure 2). Feeding rates of mussels were measured using an experimental cage setup (Figure 3). It consisted of mussels collected from natural populations immediately placed near the collection site on the funnel net (4×4 mm) of the experimental cage from which biodeposits were directed to the collection tubes below (Figure 3). Mussels were acclimatised to the caged position at the experimental site for 30 minutes prior the start of the experiment. Deployment of experimental cages lasted for 4–5 hours. Eight replicate cages were used at each location. Following retrieval, the sedimented material in the tubes was sorted immediately and biodeposits were collected with a pipette and placed into 10 ml of 96% ethanol. Individuals were packed separately into foil and deep frozen for further analysis.

Loss of chlorophyll-*a* during gut passage was measured in separate experiments in which mussels were incubated in mesocosms with natural seawater stirred by aeration. Every 30 minutes, mesocosms were thoroughly cleaned of biodeposits which were then placed into 10 ml 96% ethanol. At the end of the trial, individuals were packed into foil and deep frozen.

To estimate mussel feeding rates in their natural habitat, additional mussels were collected directly from the sea bottom at each deployment location of the funnel experiment, packed and deep frozen.

Water samples were collected from the funnel experiment sites and mesocosms to be analysed for the chlorophyll-*a* content used as a proxy for suspended microalgae, and suspended particulate matter (SPM).

Concentrations of SPM were measured gravimetrically following the methods of Environmental Sciences section 340.2 standard technique. Samples were filtered on pre-ignited (500 °C for 30 minutes) and pre-weighed Whatman GF/ F filters to estimate total suspended solid content (TSS) content. SPM was differentiated into SPIM (suspended particulate inorganic matter) and SPOM (suspended particulate organic matter) by burning the SPM filters at 500 °C for 30 minutes. The filters were cooled down on silica gel and weighed.

The contents of photosynthetic pigments were quantified spectrophotometrically in mussels, and their biodeposits and water samples using the HELCOM COMBINE Annex C-4 standard technique (Helsinki Commission, 2008). Photosynthetic pigments in the water samples were measured by ethanol extraction of particulate material collected on Whatman GF/F filters. Photosynthetic pigments in the individual mussels and their biodeposits were measured by their direct ethanol extraction. The significant fluorescence by phaeopigments was corrected by acidifying the samples with HCl which converts all chlorophyll-*a* to phaeopigments. The spectrophotometer was calibrated against 96% ethanol. Obtained values were used to calculate the chlorophyll-*a* and phaeophorbide-*a* concentrations, which were further converted to the chlorophyll-*a* equivalents (total chlorophyll-*a*) using the ratio of molar masses between chlorophyll-*a* and phaeophorbide-*a*. These were further used to calculate feeding rates of the mussels. For further details see (I).

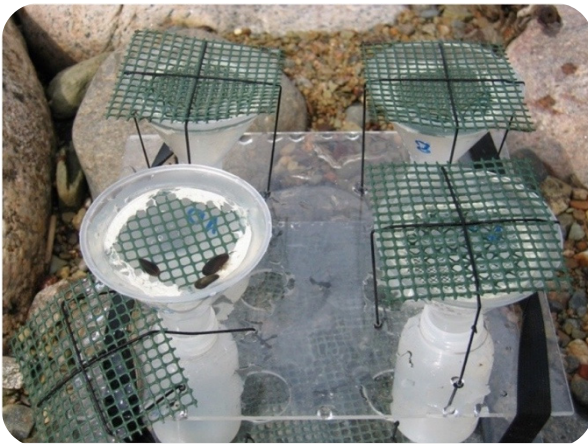


Figure 3. Detail of the experimental setup

Colonization and coexistence of *A. improvisus* and *D. polymorpha* (III) were studied in the *in situ* experiments conducted in Pärnu Bay (Figure 2). Two replicates of concrete blocks were deployed by a scuba diver along transects covering different environmental conditions in the autumn of 2011. In total, 140 blocks were deployed, of which 68% were recovered a year later with the remainder lost to wave action. Three replicates of samples were collected in the autumn of 2012 from the blocks using frames with measurements of 7×7 cm and 10×10 cm. Samples were collected from 5 levels of spatial orientation of the blocks (Figure 4), packed and deep frozen at –20 °C for further analysis. In the laboratory, samples were analysed according to the HELCOM COMBINE Annex C-9 standard technique (Helsinki Commission, 2008). Samples were sorted, all of the organisms found in the samples were counted and the dry weight of the found species was obtained after drying each species separately at 60 °C to constant weight for two weeks.

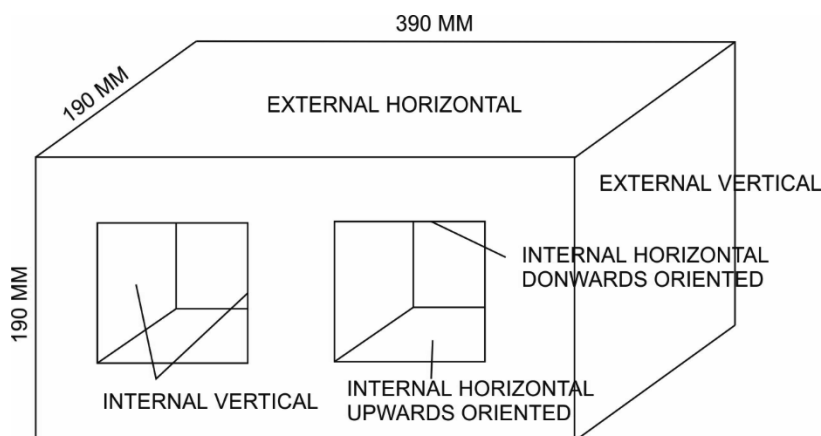


Figure 4. Scheme of the concrete block with measurements and surface orientations from which samples were collected

2.3.2. Data bank

Data on the coverage and biomass of benthos covering Estonian territorial sea was extracted from the database of the Estonian Marine Institute. Paper **II** involved analysing data from the 3585 sampling stations for the period of 2005–2009 to **measure *M. trossulus* distribution** (Figure 2). Data from 19464 sampling sites for the period of 1995–2014 were analysed to **define the assessment criteria** in paper **IV** (Figure 2). A targeted field sampling was performed in 2015 to assess quality of the habitats (**IV**).

In the predefined monitoring areas sampling sites were distributed along transects from the water edge to the maximum depth of occurrence of phytobenthic communities. In all the other areas, network of samples was randomly generated with distance between the locations varying between 100 metres and 5 kilometres, according to bottom substrate heterogeneity.

Coverage estimates of benthic macrophyte or macroinvertebrate species were obtained by means of scuba diving or underwater video. Biomass sampling and analysis followed the guidelines developed for the HELCOM COMBINE program Annex C-9 (Helsinki Commission, 2008). At each sampling site, depth, the coverage of different sediment types (rock, boulders, pebbles, gravel, sand, silt) and macrophytes (both macroalgae and higher order vegetation) were estimated either directly by diver or by remote underwater video device. The underwater camera was set at an angle of 35° below horizon to maximize the field of view and the range of the forward view was about 2 m in clear waters. The quantitative biomass samples were collected by a diver using a standard bottom frame (0.04 m²) on hard bottoms or by a quantitative Ekman-Lenz grab sampler (0.02 m²) on soft bottoms. Samples were sieved in the field on 0.25 mm mesh screens. The residues were packed and shipped directly to the laboratory of the Estonian Marine Institute, where they were

stored at $-20\text{ }^{\circ}\text{C}$. At the laboratory, subsequent sorting and counting of species was performed using a stereomicroscope and applying standard methods (Helsinki Commission, 2008). The macrobenthic species found in the samples were determined to the lowest taxonomic classification level possible. Their dry weight was obtained using scales after drying the species at $60\text{ }^{\circ}\text{C}$ for 2 weeks.

2.4. Data processing

A set of environmental variables was chosen for the analyses based on theoretical assumptions of the role of environment in suspension feeders' distribution and feeding behaviour. The near-bottom water temperature, salinity, and oxygen content in the samples of the article (I) were measured during the experiments with YSI Pro2030 multi-parameter data sonde. The Estonian Meteorological and Hydrological Institute provided wind speed data, which were corrected for the fetch during the experiments. Water was sampled to measure Chlorophyll-*a* and SPM (explained in detail in subchapter 2.3.1). The values of oxygen, current velocity (II–III) and water salinity (II–IV) were taken from the results of hydrodynamic model calculations founded on the COHERENS model from 2005–2009. The values of water chlorophyll-*a* and temperature were derived from MODIS satellite. The values of wave exposure were derived from the Simplified Wave Model (Nikolopoulos and Isæus, 2008) (II–IV). The Finnish Meteorological Institute provided ice cover over the study area for the period investigated in article II. The coverage of different sediment types was estimated either directly by the diver (II–III) or by using a remote underwater video device (III).

It should be emphasised that until recently the study area lacked major epibenthic predators and therefore the predation pressure on the epibenthos was believed to be low. Predators are mainly represented by a few molluscivorous species such as flounder and eelpout. However, an invasive harris mud crab, *Rhithropanopeus harrisi*, and roundgoby, *Neogobius melanistomus*, are actively being established in the study area, and the importance of these predators in local food webs is increasing (Kotta and Ojaveer, 2012). Roundgoby is known to feed extensively on dreissenid mussels in invaded North American rivers and on *M. trossulus* in some Baltic Sea areas. *Rhithropanopeus harrisi* is an effective predator of *M. trossulus* in the Archipelago Sea (Lokko et al., 2015) and of *D. polymorpha* in the Vistula Lagoon (Hegele-Drywa and Normant, 2009). As the abundance of these invasive species was still low during the present study, predation was not included in the distribution models.

Relationship between these environmental variables and feeding rates (I), distribution and biomass (II), and colonization (III) of BSFs was explored using a Boosted Regression Tree (BRT) predictive modelling analysis. The BRT modelling was done in the statistical software R using the gbm package.

BRT merges the notion of regression trees with the concept of boosting. Regression tree splits the data into partitions using a decision tree and appoints prediction output values for these partitions. Boosting is an ensemble method that builds a strong prediction model by successively training a set of weak prediction models to concentrate on data receiving imprecise predicted values in previous models. In the case of BRT, this large set of models is created by developing trees that handle the residuals from preceding trees, aiming to explain the variation in the data that is currently unexplained by existing trees.

A BRT model does not require prior data transformation or exclusion of outliers, being able to fit complex non-linear relationships and accommodate missing values. The model avoids overfitting the data, and by that presents a robust predictive performance. BRT models can account for spatial autocorrelation. What is meaningful in the ecological context is that it automatically deals with interaction effects between predictors. It shows the variable contributions which can be used to assess the relevance of each variable to the models. This metric gives a measure of how often the predictor is selected, and the improvement to the model, as the result of a variable being selected.

To prevent inclusion of highly correlated variables into the analysis, Pearson correlation analysis between all environmental variables was carried out preceding the modelling. If r values exceeded the critical threshold of $r > 0.7$ when collinearity begins to seriously distort model estimation and consequent prediction the variables were left out of the analysis (Dormann et al., 2013). When fitting a BRT model we used tree complexity (number of splits in each tree) equal to 5, following the suggestion of Elith et al. (2008). The model learning rate, which is the fraction of the training set observations randomly selected to propose the next tree in the expansion, was kept at 0.1 (Elith et al., 2008). Unimportant variables were dropped using a simplification tool. In order to eliminate non-informative variables, the tool progressively simplifies model, then refits the model and sequentially repeats the process until some stopping criterion is reached. Such simplification is most useful for small data sets where redundant predictors may degrade performance by increasing variance (Elith et al., 2008).

BRT model performance was assessed using cross-validation (CV) statistics calculated during model fitting which provides a measure of correlation between the recorded observations and the model fitted values (Elith et al., 2008; Hastie et al., 2009). CV values lie between 0 and 1, the larger the value – the better is the model performance.

2.5. Habitat quality assessment

In paper **IV**, we used data on coverage, abundance and biomass of benthic species to describe the quality of benthic habitats. Benthic communities are fairly stable in unaltered environments but react in critical changes as a

response to significant disturbances (Rosenberg et al., 2004). Our assessment system of habitat quality was developed based on the presence or abundance of important habitat forming species and species, which characterise stable communities.

According to the Habitats Directive Article I definition, “Reefs are hard compact substrata on solid and soft bottoms, which arise from the sea floor in the sublittoral and littoral zone, supporting a zonation of benthic communities of algae and animal species”. In paper **IV**, to establish relevant assessment criteria and reference values, habitat types were subdivided into ecological zones based on the dominance of typical species. The community structure (species composition and dominance) can notably vary within a habitat type. This is due to its wide distribution range along significant environmental gradients like depth, salinity, and wave exposure. This variation allows the division of habitat types into zones based on the dominance of typical species.

Within each habitat type, certain species have important functional roles as the habitat-forming species to maintain assemblages. Measuring the condition of certain species indicates the functional quality of the habitat because of the role that these species play (Tillin et al., 2008). A series of promising assessment criteria reflecting habitat quality, like phytobenthos/zoobenthos indices, community variables, presence of sensitive or typical species, proportions of functional or taxonomic groups, etc., were considered based on a scientific literature search. The final selection of criteria was based on ecological suitability, propriety to local conditions, occurrence rates of benthic species, response to disturbance, statistical distribution of measured values, redundancy in the context of other criteria.

Assessment of each habitat zone was based on the typical species of a given habitat. A list of typical species that are representative of stable habitats was established. Species occurrences were calculated for each habitat zone to determine typical species or higher taxonomic groups in that habitat. The value of each numeric criterion was calculated for each sampling point in the input data. Minimum, maximum and standard deviation values were calculated to further support the final selection of the criteria. The reference values were defined by comparing present-day data to the data from the 1950s–1960s, and comparing marine areas in different environmental status.

We chose hierarchical structure of assessment schemes to incorporate different priority levels of criteria. The habitat-forming species, which maintain main structural and functional properties of a habitat, were assigned to the highest priority levels in the assessment schemes.

The habitat quality was assessed based on the data collected in the year 2015. The hierarchical assessment scheme was applied for each monitoring station separately.

3. RESULTS AND DISCUSSION

3.1. Distribution patterns in relation to multiple abiotic and biotic factors

In the studied suspension feeder populations, their distribution was governed by complex interactions of physical and biological factors (Figure 5 & 6). CV estimates of predictive performance were 0.84 ± 0.04 for *A. improvisus* abundance, 0.79 ± 0.06 for *D. polymorpha* abundance, 0.85 ± 0.05 for *M. trossulus* presence, 0.65 ± 0.08 for *M. trossulus* biomass. Suitable substrate, temperature, salinity, and wave exposure were the dominant large-scale factors determining the distribution of suspension feeders in the coastal waters of the Baltic Sea (II, III).

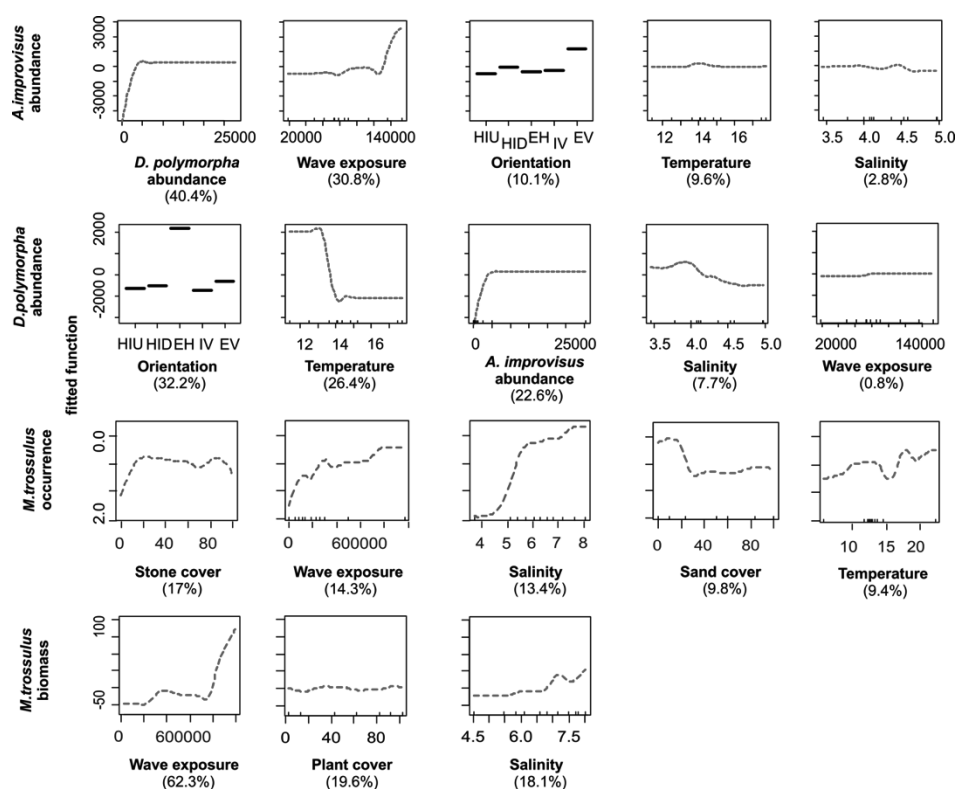


Figure 5. Standardised functional relationships between the studied species and environmental predictors. Variables are ordered by their relative contribution in the BRT model. Ticks across the bottom of each rug plot show the distribution of deciles for each predictor variable. Abbreviations: EH – external horizontal surfaces, EV – external vertical surfaces, IV – internal vertical surfaces, HID – internal horizontal downwards oriented surfaces, HIU – internal horizontal upwards oriented surfaces.

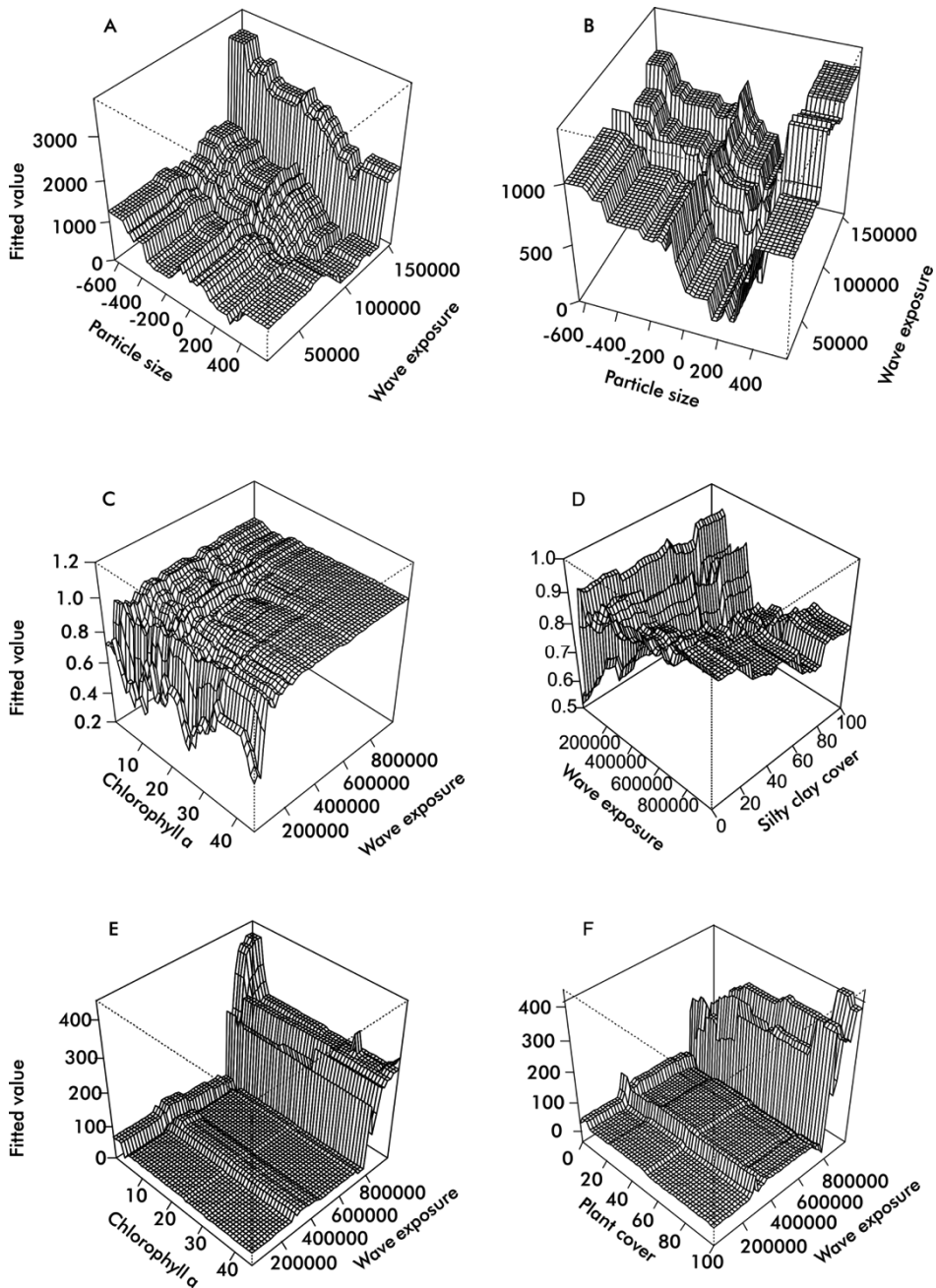


Figure 6. Three-dimensional partial dependence plots in the BRT model for (A) *A. improvisus* abundance, (B) *D. polymorpha* abundance, (C–D) *M. trossulus* occurrence, (E–F) *M. trossulus* biomass.

3.1.1. Abiotic factors

Wave exposure, one of the most important large-scale factors, significantly affected the distribution of *A. improvisus* (III) and *M. trossulus* (II) (relative contribution 30% and 14% respectively).

Abundance of *A. improvisus* was found to be significantly higher in wave-exposed areas (Figure 5) (III). Barnacles are known to thrive in wave exposed areas where increased flow velocities contribute to their passive filtration (Trager et al., 1990; Marchinko and Palmer, 2003). This pattern may also reflect an increase in larval supply with increased water flux. The effect of wave exposure was enhanced by an interaction with surrounding substrate type on barnacle and zebra mussel colonization (Figure 6A). Increased abundance of barnacles at higher wave exposures in areas with larger substrate particles is probably connected to sediment stability and mechanical disturbance by small particles. While barnacle abundance was greater on exposed solid bottoms, zebra mussels displayed high population densities at moderately and highly exposed areas with fine sediment (Figure 6B). Although zebra mussels prefer hard substrate, they are known to populate sedimentary habitats and tolerate fine suspended particles common in estuarine soft-bottom habitats (Berkman et al., 1998). It is possible that wave exposed sites are encountered more often by passively drifting settling larvae and have better food and oxygen conditions (Kobak, 2005). Evidently, artificial substrate offers additional niches that are rare in the natural surroundings with unsuitable sandy substratum. Consequently, in the presence of a suitable substrate for attachment in the sedimentary areas mussels are more successful than barnacles due to higher tolerance to increased concentrations of re-suspended fine sediment.

Wave exposure strongly influenced the presence-absence and biomass of bay mussels (relative contribution 14% and 62% respectively) (Figure 5) (II). The degree of wave exposure may determine the patterns of mussels' distribution through an indirect pathway, increasing larval colonization and the probability of recolonization in areas with elevated ice disturbance and subsequent removal of *M. trossulus* individuals (Hunt and Scheibling, 1996). Exposure and surface water chlorophyll-*a* interactively contributed to the presence of bay mussels, with chlorophyll-*a* slightly decreasing the probability of occurrence at lower exposure values but not at the highest exposure (Figure 6C). Moreover, at the high end of chlorophyll-*a* gradient the biomass of mussels was unexpectedly low (Figure 6E). Food availability is a limiting factor for benthic suspension feeders with a sedentary lifestyle but not in eutrophicated conditions (Fréchette and Bourget, 1985; Fréchette and Lefavre, 1990; Kirby and Miller, 2005). On the contrary, high amount of particles in water column may impair the feeding efficiency of suspension feeders (Alimov, 1981). Moreover, increase in phytoplankton biomass may decrease gas regime causing oxygen deficiency (Bonsdorff et al., 1997; Grall and Chauvaud, 2002). Only at elevated wave exposure, when the accumulating organic matter is constantly flushed away and oxygen conditions are improved, mussels may gain their biomass at high

chlorophyll-*a* values. Another possible explanation involves the notion that mussels in the observed area are uncoupled from the pelagic food pool, depending more on benthic diatom species (Lauringson et al., 2014). Under these conditions, mussels would rely on resuspension of benthic microalgal particles by wave action, supplying mussels with particle-rich near-bottom water. Our findings underline the importance of wave exposure as one of the main factors structuring suspension feeders' communities in the shallow coastal sea.

Substrate type significantly affected the distribution of bay mussel populations on a local spatial scale (**II**). The presence of solid substrate increased, while increasing cover of sand reduced the probability of occurrence of *M. trossulus* (Figure 5). Solid elements, such as stones and boulders, serve as the main attachment sites, offer spatial refuges and reduce predation pressure on mussels (De Blok and Geelen, 1958; Suchanek, 1978; Frandsen and Dolmer, 2002). Moreover, solid substrate slows the flow and introduces turbulence to the boundary level, which increases the amount of food available to the benthos (Fréchette et al., 1989). Decreased occurrence of mussels on fine substrate is in part related to sediment stability under strong hydrodynamic forces (Figure 6D) which can act as the direct drag force that dislodges gravel, pebbles, and resuspends fine particles. Fine particles may furthermore disturb mussel feeding, clogging its filtering apparatus with suspended particles and thereby decreasing the efficiency of food intake (Alimov, 1981; Clausen and Riisgård, 1996). Moving sands and sand scour under strong wave action may also mechanically damage animals and limit their colonisation (Menge and Sutherland, 1987).

In the presence of a suitable substrate for attachment (**III**), **microhabitat choice** significantly affected the distribution patterns of *A. improvisus* and *D. polymorpha*. Surface orientation was a very important predictor for both *D. polymorpha* and *A. improvisus* distribution (Figure 5). Surface orientations have been shown to support different types of epibiotic assemblages (Glasby and Connell, 2001; Knott et al., 2004) promoting microhabitat segregation and relieving competition in the use of habitat resources (Schmitt, 1987). The abundance of *A. improvisus* was higher on external vertical surfaces. In contrast, the abundance of *D. polymorpha* was higher on the external upper-orientated horizontal surfaces where sedimentation and wave-induced drag forces are expected to be stronger. This pattern of microhabitat choice may indicate that species avoid interspecific competition through habitat segregation (Franke and Janke, 1998; Faria and Almada, 2001). Alternatively, microhabitat segregation may be a result of multiple interaction components acting simultaneously. Larval settlement and food accessibility are stronger on the horizontal surfaces. Also, light intensity facilitates algal growth, which provides additional attachment structures for larval settlement in areas with high loads of sediments (Marsden and Lansky, 2000; Kobak, 2005). Indeed, higher rates of colonization, coupled with reduced spatial interspecific competition, can scale down the negative effect of elevated disturbance on horizontal surfaces, creating

suitable conditions for settlement and survival. However, since segregation across environmental gradients was weak, the results may imply that segregation was caused by different adaptations of species to surface orientation use.

Temperature and salinity are known to affect the presence and abundance of marine species. Both of these factors have a ubiquitous impact at the molecular level of an organism, affecting its fundamental processes like feeding, metabolism, growth and reproduction (Fong et al., 1995; Kotta et al., 2005; Tagliarolo et al., 2012). These effects can further influence their distribution through survival of the individuals (Hall et al., 1992; Karatayev et al., 1998). Temperature is also involved indirectly, determining the period of ice cover, and, as a result, partly outlines the growth season and the magnitude of ice scour (Kautsky, 1988). The contribution of temperature and salinity in explaining variability in the BSF distribution varied between species (**II**, **III**). On a local scale, average surface **temperature** was an important predictor for the zebra mussel, but not for the barnacle distribution (Figure 5). *A. improvisus* can tolerate a wide range of temperature (2–30 °C), while *D. polymorpha* is known to be more temperature sensitive. *D. polymorpha* requires temperatures between 10 and 20 °C for growth and reproduction, with an optimum at ~11 °C (Reeders and Bij de Vaate, 1990; Karatayev et al., 1998; Nasrolahi et al., 2016). Its distribution in the northern Baltic is limited by low temperatures. As average temperatures are expected to increase, climate change is likely to facilitate its spreading to the north. However, on a local scale in the observed population temperature may affect mussels more negatively compared to barnacles. On a regional spatial scale, (**III**) temperature appeared to be a mediocre predictor for bay mussel occurrence, yielding in power to substrate type, wave exposure and salinity (Figure 5).

Salinity was a stronger predictor for bay mussel and zebra mussel distribution and, to a lesser extent, for barnacle distribution. Salinity affects mussels' growth and reproduction through osmoregulation. In the study area, where salinity varies between 2.5 and 10, *M. trossulus* and *D. polymorpha* live at the edge of their salinity tolerance. Specifically, the lower salinity limit of *M. trossulus* is 4.5, while higher salinity limit of *D. polymorpha* is 6. Above its threshold, the biomass of *M. trossulus* increased sharply and levelled off at salinities over 6 (**III**). Abundance of zebra mussels increased below the salinity threshold, with a modest boost at salinities of 4 (Figure 5) (**I**). Salinity is thus a major stressor in the area, clearly limiting mussels in the studied area. Barnacles, on the other hand, are generally tolerant of a wide range of salinity but are nevertheless limited to salinities above 3–4 (Dineen and Hines, 1992; Nasrolahi, 2007).

If water salinity declines, *Mytilus* and *A. improvisus* may suffer a contraction in their distribution exacerbated by the success of *D. polymorpha*. As the distribution limits of these species shift, *D. polymorpha*, with its tolerance to low salinity and high temperature, will benefit from climate change, filling the freed niches, extending its range and becoming dominant. However,

in the areas where BSFs are already present, the importance of salinity was surprisingly marginal in explaining the abundance of zebra mussel and barnacle populations in such a stressful environment, as salinity alone explained only 8 and 3%, respectively, of total variability in abundance compared to other factors for mussels and barnacles. On the other hand, salinity was an important predictor of bay mussel biomass, which might be linked to osmotic stress limiting *M. trossulus* size. This may indicate that the stressor determining the distribution limits may have only a minor impact on the abundance within these limits. Salinity may define the range of the species, but other physiological stressors may govern the abundance of populations inhabiting conditions near their physiological tolerance limits. Furthermore, within its suitable habitat range, salinity may have an important impact on the structure of the populations influencing biomass distribution of species with a strong stress-dependency of size. However, we can only speculate on the processes behind the observed patterns, which can be related to a number of other unstudied factors influencing BSF populations.

3.1.2. Biotic factors

In addition to abiotic factors, **biotic interactions** shape the suspension-feeding communities. The algal cover is an influential factor for bivalves. Macroalgae are not only known to compete with mussels for spatial resources but they also increase the complexity of the substrate and serve as attachment structures for the mussels at sites with high sediment loads (Dobretsov, 1999; Westerbom et al., 2008). Mussels are generally known to be remarkable spatial competitors, outcompeting macroalgae (Westerbom et al., 2008). However, in the study area, the increase in plant cover positively affected the occurrence and biomass of bay mussels (**II**). The lowest probability of finding mussels was at sparsely vegetated or unvegetated bottoms (Figure 6). Mussel biomass dramatically increased with plant cover at exposed locations, while at less exposed areas the highest biomass occurred when vegetation was scarce (Figure 6F). Under moderate disturbance, spatial competition may be playing a role in less exposed areas. Here *M. trossulus* may recover from disturbance like storms or ice scour more quickly than canopy-forming macroalgae and thereby gains a competitive advantage, whereas at higher stress conditions, there can be facilitative interactions between mussels and macrophytes. Macroalgae increase the complexity of the substrate and can function as attachment structures for the mussels at sites with high sediment loads. Algae create a heterogenic environment and refuges from environmental stress, dampening different types of disturbances (Dittman and Robles, 1991). At the same time, mussels are known to facilitate the growth of macroalgae by providing extra nutrients for them. Thus, mutualistic interactions between mussels and macroalgae may actually outweigh potential competition between them. However, interspecific interactions may be indirectly affected by the projected reduction of ice cover.

Moderate ice disturbance dislodges a proportion of epibenthos, clearing out space and promoting co-existence of species. In the absence of such disturbances, competition is expected to intensify, favouring fast growing species.

Interactions between introduced species have received less attention than the effects of introduced species on native ones. After all, the potential damage that introduced species may inflict on native species is more concerning to conservationists and resource managers. Likewise, biotic interactions between barnacles and mussels in their invaded area are poorly studied. In the areas where both *D. polymorpha* and *A. improvisus* coexist, *A. improvisus* may be a more successful fouler than *D. polymorpha* and they compete for space and food as in the case of *M. edulis* (Dürr and Wahl, 2004). Despite the spatially limited sessile lifestyle of the studied species, we saw no evidence of strong competition in their distribution patterns. On the contrary, increase in one species predicted an increase in the abundance of the other, especially for barnacles – mussel abundance was the best predictor of barnacle abundance over other factors (Figure 5). This can be related to unmeasured environmental variables favouring both species in similar ways, but also to positive settlement cues from the other species. The cases of positive interactions between nonindigenous species can lead to “invasional meltdown” in recipient communities (Simberloff and Von Holle, 1999). This might be a possibility in our study area. The observed relationship is unequally reciprocal, as our results indicate that zebra mussels may create more favourable environments for barnacles than vice versa. In the steady-state ecosystem, their interaction depends probably on abiotic conditions and a successional sequence of species (Järvekülg, 1979; Laihonen and Furman., 1986; Dürr and Wahl, 2004). Barnacles may begin the chain of ecological succession that eventually leads to mussels overgrowing barnacles. Barnacles are known to attach to mussel shells using them as a secondary substrate, which can reduce the growth of mussels that need to invest more energy into byssus production (Buschbaum and Saier, 2001). It could be assumed that this is less advantageous for mussels that are more easily dislodged from the substrate due to increased mass. This may also explain why mussels are more abundant on horizontal surface orientations (Figure 5).

Current distribution of syntopic species merit attention in the context of the future success of invasive species. Climate change may cause shifts in size structure, spatial range and abundance of populations, leading to altered species interactions and changes in community structure. Our results can be used to enhance the design of monitoring programs, control of invasive species, and integrated management of vulnerable biota and their habitats. They emphasise the importance of ecosystem-based management and the necessity to consider not only environmental limitations but also interspecific interactions, as well as the design of subsidiary structures, which can all modify the structure of colonising communities.

3.2. Feeding behaviour in relation to environmental factors

The feeding rates of *D. polymorpha* were related to site-specific environmental parameters. While the distribution of the *D. polymorpha* population in the Pärnu bay was mostly affected by substrate, temperature and salinity (Figure 5) (III), biodeposition of this species showed a strong relationship with water chlorophyll-*a* concentrations, salinity, and wind conditions in the bay, and only marginally with the ambient water temperatures (I) (Figure 7). Cross-validated correlation estimate of the model performance was 0.62 ± 0.06 .

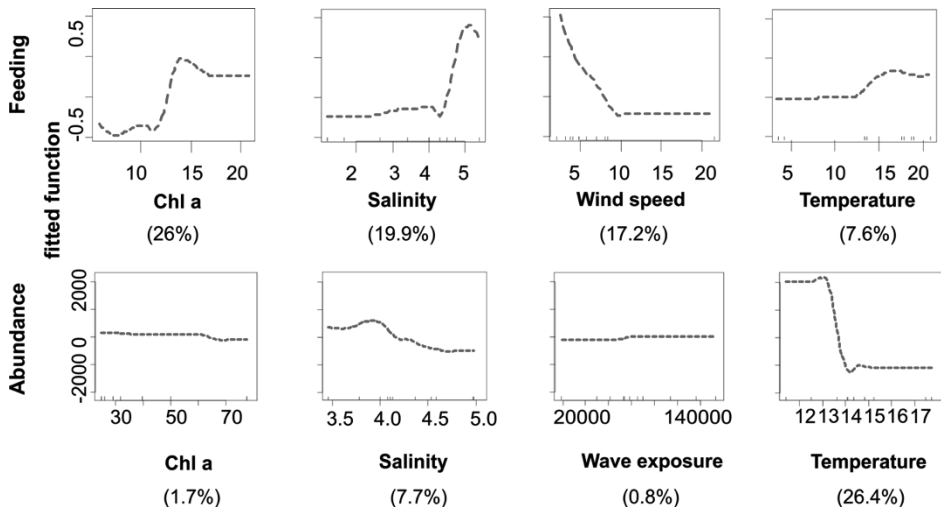


Figure 7. Functional relationships between the studied environmental variables, *D. polymorpha* feeding and distribution. Variables are ordered by their relative contribution on the biodeposition rates in the BRT model.

As expected, increased chlorophyll-*a* concentrations had a positive effect on the feeding rates of zebra mussel up to the threshold of $15 \mu\text{g l}^{-1}$ of water chlorophyll-*a* content. A further increase in chlorophyll-*a* concentrations did not lead to further increase in feeding, which reached a plateau. Feeding rates of zebra mussels are known to increase with the amount of food until a threshold, dropping when incipient limiting concentrations of food are obtained (Fanslow et al., 1995; Clausen and Riisgård, 1996; MacDonald and Nodwell., 2003). However, our results indicate that zebra mussel feeding rates did not drop at $5\text{--}10 \mu\text{g l}^{-1}$, as previously recorded (Kotta et al., 2005). In our experiment, chlorophyll-*a* concentration threshold is at least one-third higher than earlier observed. In contrast, *D. polymorpha* colonization was practically unrelated to chlorophyll-*a* concentrations (Figure 5 and 7). Differences in functional responses to chlorophyll-*a* are most probably related to the elevated eutrophication that results in increased level of suspension concentration. This has a minor effect on their distribution, possibly due to overriding importance of

other factors. However, even in eutrophicated conditions chlorophyll-*a* concentrations define the feeding of *D. polymorpha*.

Salinity had a significant impact on the feeding activity of zebra mussels. Zebra mussels exhibited an exponential increase in feeding with increasing salinities. Its distribution peaked at salinity value 4 and showed a marked decline above these values, whereas the ingestion rates were particularly striking at salinity values 4.5–5, the highest levels of salinity tested. The studied population seems to be well acclimated to slightly higher salinity conditions than in its native distribution range, while salinity extremes at the range edge do not seem to affect the feeding performance of mussels. This tolerance may be achieved in part by the high food availability that enables it to cope with stress induced by extreme salinity. The distribution of the population may be determined by salinity impact on other features than feeding, such as osmoregulation.

A more ambiguous, but nevertheless influential, environmental factor affecting mussel feeding is wind-induced disturbance. Interactive impact of wind speed and chlorophyll-*a* concentrations on feeding was noticeable, with ingestion rates maximal at reduced wind velocities and elevated food concentrations (Figure 8). Because the bay is shallow with predominantly soft clay and sandy mud sediments, wind forcing induces mixing and resuspension of particulate material, which are important for the flux of particles in the shallow waters. The increased dilution of available food by resuspended matter may impede mussels' feeding, leading to decreased assimilation efficiency and energy intake (Alimov, 1981). These particles presumably clog the feeding apparatus of the mussels (Pascoe et al., 2009; Zaiko and Daunys, 2011), which might explain a strong negative exponential relationship between mussel feeding rates and wind in our experiments. The organic fraction of suspended sediments can represent an important source of food and, in this case, high concentrations of suspended sediment would not decrease the filtering of mussels. Nevertheless, more straightforward suspended particulate matter (SPM) estimated from the water column did not explain variance in mussel feeding as much as more intricate and complex wind speed (Figure 9). Lighter clay particles may be sustained in the suspended conditions for a prolonged time after the reduction of wind-induced disturbance, thereby uncoupling the impact of active wind speed from suspended particulate inorganic matter (SPIM) values. On the other hand, heavier particles like sand are likely to sink sooner after the weather has settled and are therefore directly related to wind speed. Thus, the pronounced adverse effect of strong winds compared to SPIM may be related to more abrasive suspended sand being less favourable for mussels than suspended lightweight particles.

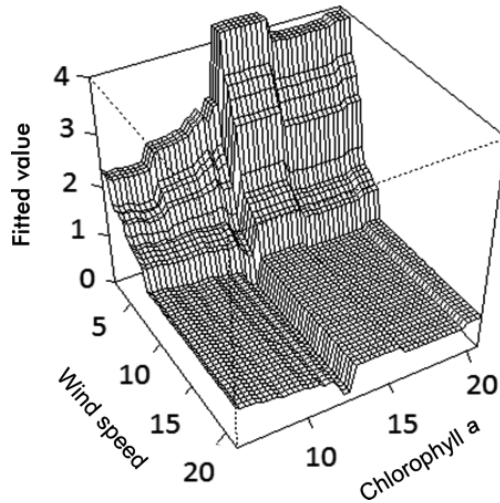


Figure 8. Three-dimensional partial dependence plot in the BRT model for *D. polymorpha* feeding rates

Other observed variables were less important predictors of feeding rates of *D. polymorpha* (Figure 9) and explained less variability than any two of the top three predictors (Figure 7).

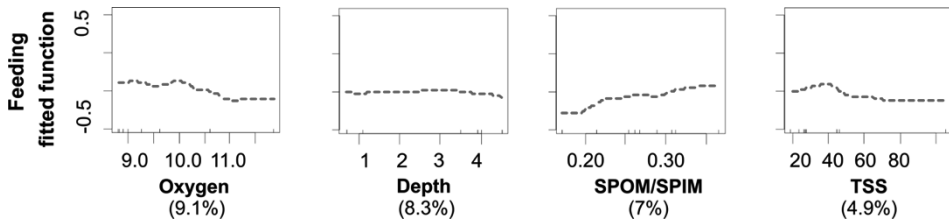


Figure 9. Functional relationships between environmental predictors and feeding rates of *D. polymorpha*

We may expect zebra mussel populations to continue benefiting from increasing primary production because of nutrient enrichment due to changes in precipitation and runoff patterns in the Baltic Sea. On the other hand, projected increase in storm frequency can be expected to have a negative impact on the feeding of mussels through increased sediment resuspension inhibiting their feeding activity. Moreover, feeding activity of the observed mussel population may not benefit from increased precipitation and decrease in salinity, although, on the contrary, its distribution might (Andersson et al., 2015; Holopainen et al., 2016).

Use of non-native filter feeders to enhance water quality in estuarine environments offers considerable potential for water quality management (McLaughlan and Aldridge, 2013). Yet, when considering manipulation

measures it is necessary to account for species habitat requirements as well as factors that can affect their settlement and filtration. Our results can be used as a background information when choosing the right sites with optimal distribution and filtration conditions for successful cultivation of zebra mussels. These results may also be used in non-indigenous species (NIS) risk assessments and monitoring plans, to identify sites that are vulnerable to invasions and the success or failure of NIS following their introduction.

3.3. Suspension-feeders' habitat quality

In article IV we present an example of using scientific data for conservation purposes. The method for the assessment of habitat quality is partly explained in the Material and Methods section 2.5. We define BSF habitat through ecological zonation of the HD habitat “reefs” (code 1170), assign relevant assessment criteria and favourable reference values based on biomass, abundance and coverage of benthic species, and assess habitat quality in the Estonian sea.

To account for the possible variability in the community structure along environmental gradients, ecological zoning was established for the habitat “reefs” based on the dominance of typical species (IV). The typical dominant species in this habitat type are *Fucus vesiculosus*/*Fucus radicans*, *Furcellaria lumbricalis*, epifaunal bivalves (*Mytilus trossulus*, *Dreissena polymorpha*), and barnacles (*Amphibalanus improvisus*) (Paal, 2007). Based on these species, habitat types were classified into three zones: *Fucus* belt; red algae belt; and benthic suspension-feeders' belt (BSFs' belt).

The BSFs' habitat zone was assigned to a depth of 5–20 metres (IV). It is characterised by a high heterogeneity of bottom substrates comprised mainly of stones and boulders, which may alternate with patches of sand, gravel, and moraine. Due to this variability in the coverage of substratum the distribution of the dominant organisms is also considerably irregular: patches lacking attached organisms fill in for densely colonised areas with bay mussels, barnacles or zebra mussels. Vegetation in this zone is generally poor, consisting mainly of filamentous algae. Seasonal mass occurrence of filamentous algae in this habitat, which is mainly related to eutrophication, promotes seasonal outbreaks of herbivorous invertebrates. Also, polychaetes and mobile crustaceans like amphipods and mysids inhabit this zone. Coverage of mussels or barnacles should be at least 1% or alternatively, their biomass should be 6 gm⁻². If other reef forming species like *Fucus* spp. and *F. lumbricalis* contribute more than 10% of the total biomass or their coverage constitutes more than 5%, then the habitat type should be classified to *Fucus* belt or red algae belt, respectively.

In order to assess the quality of BSFs' belt, we developed hierarchical assessment scheme based on the relevant selected criteria (Figure 10). Habitat quality was assessed based on the three criteria: (a) presence of suspension-feeders compared to reference conditions, (b) presence of at least one highly

sensitive zoobenthos taxon, (c) presence of gastropods, amphipods or isopods. However, it should be emphasised that these criteria cannot be used in the aphotic zone. Although BSFs may inhabit aphotic zone, here a benthic community will lack typical animals other than mussels and barnacles. This does not indicate an unfavourable status of the habitat but rather signifies that the hydrodynamic active deep marine areas are essentially devoid of algae and herbivorous animals associated with them. Unfortunately, we lack biomass data from the areas deeper than 20 metres and, thus, couldn't determine relevant criteria for the habitats in the deeper aphotic areas.

The usefulness of the application of the assessment schemes depends on demonstrating that the selected criteria accurately indicate variability in quality conditions, and that these criteria have ecological relevance. The critical factor is presence of BSFs in comparison with previous monitoring period (a). In general, the presence of dominant species demonstrates the lack of significant deterioration of the habitat and indicates that habitat function is being maintained. The assumption is that as organic input to the sediment increases, populations of BSFs decline and deposit-feeders start dominating communities (Pearson and Rosenberg, 1978). The loss of a habitat-forming species means that the quality of the habitat has deteriorated to bad and the habitat can't support viable populations. Next, highly sensitive zoobenthos taxa (b) are typical to a stable community, they are non-tolerant to increased nutrient load and they usually inhabit only pristine sites, e.g. *Monoporeia affinis*, *Mysis* spp, *Saduria entomon*. Finally, functional diversity accounts for relationships between organisms that are important in structuring ecosystems. Gastropods, amphipods and isopods (c) fulfil specific ecological functions in communities, e.g. gastropods are herbivores that graze on biofilm while mobile amphipods consume macroalgae. The most common gastropods in the given habitat are the river nerite (*Theodoxus fluviatilis*) and mudsnail (*Peringia ulvae*); the most common amphipods belong to the crustacean genus *Gammarus*; and the most common isopods are crustaceans belonging to the *Idotea* genus and *Jaera albifrons*. We expected all of the criteria to be satisfied for the habitat to correspond to a good quality status (Figure 10). 10 out of 11 assessed monitoring stations were in good status. The station that was assessed to be in bad status didn't have any highly sensitive zoobenthos taxa present.

Best available scientific data covering both spatial and temporal scales was used for assessing habitat quality. Although data used in this assessment cover roughly 20 years of research there are clear limits to these data application, e.g. in the aphotic zone. Based on our example, scientific information can be used effectively in the habitat assessment, but more scientific data are clearly needed for a comprehensive evaluation. This emphasises the importance of strong monitoring programs which consider specific conservation biology goals in the ongoing data collection.

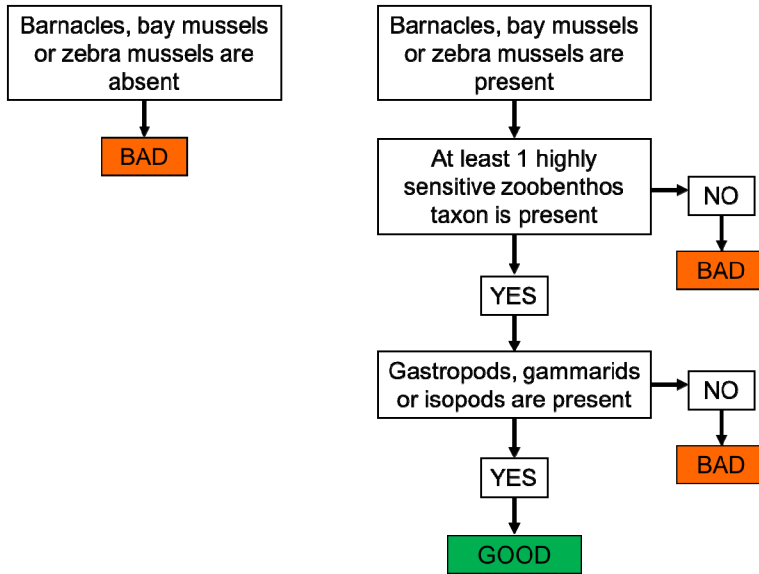


Figure 10. Assessment criteria and reference values for the suspension-feeders' zone (at depths 5–20 m) in the habitat type Reefs (code 1170)

CONCLUSIONS

- I. Our *in situ* experiments (I) showed that zebra mussel feeding was mainly explained by **chlorophyll *a* concentrations (26%), salinity (20%) and wind-induced disturbances (17%)**. Temperature, oxygen and SPM concentrations were less important predictors of mussel feeding. The study showed that mussel feeding was principally food regulated even in a highly eutrophic system. This supports their potential value as biofilters in the manipulation of eutrophic waterbodies.
- II. Distribution of *M. trossulus* (II) was mainly explained by **substrate availability**. Once suitable substrate was available, **wave exposure and salinity** limited the presence and biomass of bay mussels. **Biotic interactions** with macroalgae affected biomass of bay mussels, suggesting mutualistic interactions between them. These results provide a useful basis for predicting future bay mussel distribution and biomass in the Baltic sea in the changing climate conditions. They emphasise the importance to consider not only environmental limitations but also interspecific interactions when designing monitoring programs.
- III. Coexistence of *A. improvisus* and *D. polymorpha* was very strongly affected by the **orientation of the substrate (III)**. Zebra mussels preferred exposed vertical surfaces, while bay barnacles preferred vertical ones. We saw no evidence of strong competition between studied species. On the contrary, species were facilitating each other's colonization. These **biotic interactions** between zebra mussels and bay barnacles played an important role in their distribution. However, the interaction was unequally reciprocal, since it was the most important predictor for bay barnacle abundance but not for zebra mussel. The study provides experimental evidence that the location and design of underwater artificial structures can determine or modify the structure of colonising communities. These results can be considered when designing artificial structures for monitoring or biomanipulation purposes in the respective sea area.
- IV. Habitat quality was assessed based on three criteria: (a) presence of BSFs, (b) presence of at least one highly sensitive zoobenthos taxon, (c) presence of gastropods, amphipods or isopods (IV). Hierarchical schemes were applied to assess the quality of BSFs' habitat, which was evaluated to be good at 10 out of 11 monitoring stations. The use of existing scientific data provides a robust foundation for habitat quality assessment. The outputs satisfy practical conservation needs as well as provide policy makers with relevant information. However, supplementary studies should be conducted in the deeper areas in order to have data on the habitats in aphotic zone.

SUMMARY

Benthic suspension feeders (BSF) are an important ecological guild in coastal ecosystems, functioning as a natural biological filter and providing habitat and food for other species. However, human activities are causing rapid changes in coastal ecosystems with a wide range of ecological responses of species and communities. Detailed knowledge of the ecology of BSF species is highly important for human pressure mitigation.

In this thesis, three species of BSF were chosen as research objects: the non-indigenous *Amphibalanus improvisus* and *Dreissena polymorpha*; and the native *Mytilus trossulus*. Although effects of *D. polymorpha* invasion are well documented, relative contribution of different environmental variables to *D. polymorpha* feeding remains under-examined. Moreover, there is no quantitative information on coexistence of *D. polymorpha* and *A. improvisus* in their invaded range, despite their ubiquity and expanding research on non-indigenous species. Equally important, distribution of native *M. trossulus* along different environmental gradients has not yet been fully understood and needs further research. This knowledge is crucial for development of conservation actions and management plans.

In this thesis, I explore how various environmental gradients and biotic interactions affect BSF communities. First, we quantified the contribution of environmental factors on the feeding of *D. polymorpha*. Then we studied the colonization and coexistence of *D. polymorpha* and *A. improvisus* in response to environmental forcing on a local scale. Next, we determined the contribution of these factors on the distribution and biomass of *M. trossulus* on a larger spatial scale. Finally, we evaluated habitat quality of these species on a national level using existing scientific data.

In order to analyse feeding behaviour, grazing rates of *D. polymorpha* were derived from field populations by measuring the content of algal pigments in specimens and their biodeposits in their natural habitat as well as separate mesocosms. The results suggest that mussel feeding behaviour is principally food-regulated even in a highly eutrophic system. High food levels may enable mussels to cope with stress induced by elevated salinity. Wind-induced sediment resuspension processes elicit strong inhibitory effects on feeding, depending on the intensity of disturbance and the edible contents of the suspended material.

Colonization of *A. improvisus* and *D. polymorpha* on a local scale was studied in *in situ* experiments using artificial substrate. The results showed that local colonization was structured by species-specific microhabitat use coupled with both individual and interactive effects of environmental gradients. Mussels strongly preferred horizontal surfaces, and their colonization was best explained by temperature. Instead, barnacles were more abundant on vertical surfaces and their colonization was best explained by wave exposure. Biological interaction between the studied species was another important structuring component. No

evidence of strong competition in distribution between these species was observed. Reciprocal abundances of barnacles and zebra mussels was a positive predictor for their abundances.

To explain the distribution and biomass of *M. trossulus* on a larger scale, we analysed existing data on the occurrence and biomass of *M. trossulus* for the period of 2005–2009 in the Estonian coastal sea. Data were obtained by means of scuba diving and biomass sampling or underwater video and stored in the database of the Estonia Marine Institute. Distribution patterns of *M. trossulus* were largely driven by separate effects of direct environmental gradients and interactive effects of resource gradients with direct environmental gradients. The increasing cover of boulders, elevated wave exposure and salinity, as well as moderate ice disturbance, increased the probability of occurrence of *M. trossulus* in the study area. Biological interactions most probably reflected either facilitative interactions between mussels and macrophytes or co-variance due to a common stressor. Within its suitable habitat range, the biomass of *M. trossulus* was primarily a function of resource gradient. The results suggest that over a larger scale, direct environmental gradients seem to define the distribution pattern of *M. trossulus*, and within the favourable distribution range, resource gradients in interaction with direct environmental gradients are expected to set the biomass level of mussels.

As an example of application of scientific data for conservation purposes we evaluated BSFs' habitat quality based on the best available scientific data. We used data for the period of 1995–2014 to define the relevant assessment criteria in the Estonia coastal sea. Criteria to assess the quality of BSFs' habitat were based on scientific literature and were chosen to be presence or absence of suspension-feeders in comparison to previous assessment period, presence of highly sensitive zoobenthos taxa, presence of gastropods, amphipods or isopods. Based on ecological relevance we assigned importance levels to these criteria and established a hierarchical system of assessment. We evaluated BSFs' habitat to be in good status in 10 out of 11 stations based on the data collected in 2015.

SUMMARY IN ESTONIAN

Hõljumtoiduliste põhjaloomade levik, toitumine ja elupaik madalas rannikumeres

Hõljumtoidulised põhjaloomad on tähtis funktsionaalne rühm rannikuökosüsteemides. Neist Läänemeres tähtsaim on söödav rannakarp (*Mytilus trossulus*). Magestunud lahtedes esineb arvukalt rändkarpe (*Dreissena polymorpha*). Väiksematest hõljumtoidulistest põhjaloomaliikidest on arvukaim harilik tõruvähk (*Amphibalanus improvisus*). Nad on looduslikud biofiltreerijad ja ökosüsteemi insenerid, pakkudes elupaika ja toitu teistele organismidele.

Inimtegevus ohustab rannikuökosüsteeme mitmel moel. Peamisteks ohuteguriteks on eutrofeerumine, võõrliigid ja kliimamuutused. Põhjalikud teadmised liikide ökoloogiast on seega aktuaalsemad kui kunagi varem. Kuigi võõrliigid mängivad tähtsat rolli rannikumere ökosüsteemis, tänaseni pole uuritud hõljumtoiduliste võõrliikide kooseksisteerimist. Samuti on vähe uuritud erinevate keskkonnategurite mõju hõljumtoiduliste põhjaloomade toitumisele ja levikumustrite kujunemisele eutrofeerunud Läänemere tingimustes. Nimetatud teadmised on oluliseks alustalaks rannikumere looduskaitse tegevuste toetamiseks.

Käesoleva doktoritöö eesmärk on uurida, kuidas erinevad abiootilised ja biootilised tegurid ning nende interaktsioonid mõjutavad hõljumtoiduliste põhjaloomade levikut, toitumist ja kooseksisteerimist ning mis on nende elupaikade seisund Eesti vetes.

Toitumise hindamiseks muutuvates keskkonnatingimustes (I) korraldasime *in situ* ja *ex situ* katseseeriad looduslikest populatsioonidest kogutud rändkarbiga, kes on võõrliik. Katsed viidi läbi Pärnu lahes, mis on tugevalt eutrofeerunud veekogum. Planktonvetikad on liigi põhiline toiduallikas ja seega kasutasime vetikapigmenti klorofüll-a liigi toitumise indikaatorina. Laboritingimustes analüüsisime vetikapigmentide sisaldust vees, rändkarpides ja nende väljaheidetes ning arvutasime selle põhjal rändkarpide toitumismäärad. Tulemused näitasid, et isegi tugevalt eutrofeerunud veekogus sõltus rändkarpide toitumine peamiselt toidu kättesaadavusest. Tõenäoliselt aitab just toidurohkus rändkarbil toime tulla tema soolsustaluvuse ülapiiri tingimustes. Tuulest põhjustatud setete resuspensioon, selle tugevus ja hõljumi sisaldus veesambas mõjutavad samuti rändkarbi toitumist.

Hõljumtoiduliste põhjaloomade kinnitumise ning keskkonnatingimuste vaheliste seoste uurimiseks (III) paigutas sukelduja erinevatesse Pärnu lahe piirkondadesse betoonist tehissubstraadid. Aasta hiljem koguti substraatidelt prooviraamiga proovid ning määrati nendes hõljumtoiduliste põhjaloomade arvukus ja biomass. Pärnu laht on oma madala soolsuse poolest rannakarbi jaoks ebasobiv piirkond. Seega võrdlesime ainult rändkarbi ja tõruvähi kinnitumiseelistusi, kes on mõlemad võõrliigid. Tulemused näitasid, et loomade kinnitumist määrasid tehissubstraadi pinnaorientatsioon ja erinevad keskkonnategurid. Rändkarpi mõjutas kõige rohkem temperatuur, tõruvähki aga

avatus lainetusele. Rändkarp oli nõudlikum pinnaorientatsiooni suhtes, eelistades horisontaalseid pindasid, tõruvähk oli aga arvukam vertikaalsetel pindadel. Samuti mõjutas ühe liigi arvukus positiivselt teise liigi arvukust.

Rannakarpide levikumustrite kirjeldamiseks (II) kasutati olemasolevate arvukuse ja biomassi andmete põhjal *Boosted Regression Trees* masinõpe modelleerimist. Loodud mudelid näitasid, et põhjasubstraat, avatus lainetusele ja soolsus mängivad Eesti meres rannakarpide leviku kujundamises põhirolli. Bioloogilised interaktsioonid põhjataimestikuga mõjutasid rannakarpide biomassi nende elupaiga ulatuses.

Hõljumtoidulised põhjaloomad on Euroopa Liidu loodusdirektiivi karide elupaigatüübi (kood 1170) ühed tunnusliigid. Selleks, et hinnata antud elupaiga seisundit (IV), me kasutasime varasemalt kogutud teadusliku andmestiku. Me määratlesime seisundi hindamise kriteeriumid ning töötasime välja ja katsetasime hindamismetoodikat. Elupaigatüüp jagati ökoloogilisteks võõnditeks tunnusliikide või rühmade domineerimise alusel. Hõljumtoiduliste põhjaloomade võõndiks määrati 5–20 meetri sügavusel asuv kivise merepõhajaga elupaik, kus põisadru või agariku biomass on <10%. Kuigi hõljumtoiduliste põhjaloomade võõnd võib levida afootilisse tsooni, käsitleti selles töös ainult footilise tsooni elupaikasi. Potentsiaalsete kvaliteedi kriteeriumitena testiti erinevaid merepõhja taimestiku ja selgrootute indekseid, koosluse muutujaid, tundlike või tüüpiliste liikide olemasolu, liikide/rühmade osakaalusid. Sobivateks valiti tunnusliikide olemasolu, tundlike liikide arv ja iseloomulike taksonoomiliste või funktsionaalsete rühmade olemasolu. Heas seisundis elupaigas peaks olema esindatud: a) tunnusliigid – söödav rannakarp, tavaline tõruvähk või rändkarp; b) vähemalt üks reostuse suhtes kõige tundlikum loomaliik – näiteks merikilk (*Saduria entomon*); c) vähemalt üks järgmistest taksonoomilistest rühmadest: teod, kirpvähilised või kakandilised. Valitud kriteeriumite põhjal ehitati hierarhilise hindamissüsteemi, kus kõrgem tähtsustase oli määratud tunnusliikidele. 2015 aastal kogutud andmete põhjal hinnati hõljumtoiduliste põhjaloomade elupaiga seisundit heaks kümnes jaamas üheteistkümnest.

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PUBLICATIONS

CURRICULUM VITAE

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Education

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1993 – 2005 Tallinn High School of Humanities
1993 – 2001 Nõmme Music school for children

Professional career

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2013 – 2016 Research Assistant, Estonian Marine Institute, University of
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2010 – 2013 Lab specialist, Estonian Marine Institute, University of Tartu

Language skills

Estonian C2, Russian C2, English C2, Spanish A1

Research interests

Marine benthic habitats, benthic suspension feeders

Scientific publications

Torn, K.; Herkül, K.; Martin, G.; Oganjan, K. (2017). *Assessment of quality of three marine benthic habitat types in northern Baltic Sea*. Ecological Indicators, 73, 772–783.
Oganjan, K.; Lauringson, V.; Kotta, J.; Rostin, L.; Martin, G. (2016). *Factors affecting the recruitment of Amphibalanus improvisus and Dreissena polymorpha in a highly eutrophic brackish bay*. Estuarine, coastal and shelf science, 184, 37–45.
Oganjan, K.; Reialu, G.; Martin, G.; Herkül, K.; Torn, K. (2016). *What lies beneath the sea?* Eesti Loodus, 67 (10), 12–17.
Kotta, J.; Oganjan, K.; Lauringson, V.; Pärnoja, M.; Kaasik, A.; Rohtla, L.; Kotta, I.; Orav-Kotta, H. (2015). *Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of Mytilus trossulus in a brackish non-tidal environment*. PlosOne, 10 (8), e0136949, journal.pone.0136949.

- Pajusalu, L.; Martin, G.; Paalme, T.; Põllumäe, A.; Oganjan, K. (2015). *Ocean acidification poses grave danger to marine ecosystems*. Eesti Loodus, 66 (9), 8–14.
- Oganjan, K.; Lauringson, V. (2014). *Grazing rate of zebra mussel in a shallow eutrophicated bay of the Baltic Sea*. Marine Environmental Research, 102, 43–50.
- Oganjan, K.; Virro, T.; Lauringson, V. (2013). *Food spectrum of the omnivorous rotifer *Asplanchna priodonta* in two large northeastern European lakes of different trophic level*. Oceanological and Hydrobiological Studies, 42 (3), 314–323.

Additional coursework

- Practical course, *Winter School of Ecology, Winter Limnology*, University of Jyväskylä, Lammi, Finland, 2009
- Extracurricular training, *Statistical Modelling in Natural Sciences*, Doctoral School of Earth Sciences and Ecology, University of Tartu, Tartu, Estonia 2010
- Workshop, *Higher Plants and Mosses in the Baltic Sea*, Askö, Sweden, 28–30.5.2012
- Practical course, *Ecophysiology of Macroalgae*, Aarhus, Denmark 2013
- Practical course, *Physical/Biological ocean interactions: from the micro to the large scale*, The Ramon Margalef Summer Colloquia, Barcelona, Spain 2013
- Practical course, *English for Academic Purposes (B2/C1)*, 20 academic hours, University of Tartu, Tallinn, Estonia 27.03-24.04.2015
- Practical course, *Persuasive public speaking*, Alfa-Omega Communications OÜ, Tallinn, Estonia 11–12.01.2017
- Practical course, *Map Info basics*, Reach-U As, Tallinn, Estonia 7–8.02.2017

Awards and scholarships

- 2013 NordForsk scholarship, Nordic Network for Marine Inventories and Modelling, Nordic Council of Ministers
- 2013 Travelling grant from the Doctoral School of Sciences and Ecology 2009–2015, University of Tartu
- 2013 Kristjan Jaak scholarship, short-term assignment abroad, Ministry of Education and Research, Archimedes Foundation, European Union Social Fund
- 2013 ESF DoRa T8 scholarship, participation of young researchers in the international exchange of knowledge, Archimedes Foundation, European Union Social Fund
- 2014 Travelling grant from the Doctoral School of Sciences and Ecology 2009–2015, University of Tartu
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Conference presentations

Oral presentation “*Preserving Baltic Sea biodiversity – continuous challenge on the scene of increasing human pressures and climatic variability.*” Baltic Sea Conference, Estonian Water works association, Stockholm, Sweden, 19.05.2016

Oral presentation “*Changes in the Baltic Sea within the last 25 years*“, The 9th International Conference of the UNESCO Baltic Sea Project „Science of Changes, Pirita SPA ja conference hotel, Tallinn, Estonia 6.06.2015

Poster presentation “*Factors affecting zebra mussel distribution on artificial substrate*“, Aquatic Science Meeting, ASLO, Granada, Spain, 22–27.02.2015

Poster presentation “*Benthic communities on artificial reefs in relation to spatial orientation and surface roughness in a eutrophicated bay of the Baltic Sea*“, 43rd Annual Benthic Ecology Meeting, University of North Florida, Jacksonville, USA, 20–22.03.2014

Oral presentation “*Grazing impact of zebra mussel in a shallow eutrophicated bay of the Baltic Sea*“, European Marine Biology Symposium, National University of Ireland, Galway, Ireland, 19–23.08.2013

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Publikatsioonid

Torn, K.; Herkül, K.; Martin, G.; Oganjan, K. (2017). *Assessment of quality of three marine benthic habitat types in northern Baltic Sea*. Ecological Indicators, 73, 772–783.
Oganjan, K.; Lauringson, V.; Kotta, J.; Rostin, L.; Martin, G. (2016). *Factors affecting the recruitment of Amphibalanus improvisus and Dreissena polymorpha in a highly eutrophic brackish bay*. Estuarine, coastal and shelf science, 184, 37–45.
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Kotta, J.; Oganjan, K.; Lauringson, V.; Pärnoja, M.; Kaasik, A.; Rohtla, L.; Kotta, I.; Orav-Kotta, H. (2015). *Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of Mytilus trossulus in a brackish non-tidal environment*. PlosOne, 10 (8), e0136949, journal.pone.0136949.

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Saadud uurimistoetused ja tunnustus

- 2013 NordForsk stipendium, Nordic Network for Marine Inventories and Modelling, Nordic Council of Ministers
- 2013 Maateaduste ja Ökoloogia doktorikooli stipendium, Tartu Ülikool
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Täiendõpe

- Praktiline kursus, *Winter School of Ecology, Winter Limnology*, University of Jyväskylä, Lammi, Soome 2009
- Täiendusõpe, *Statistilised mudelid loodusteaduses*, Maateaduste ja Ökoloogia doktorikool, Tartu Ülikool, Tartu, Eesti 2010
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- Suuline ettekanne “*Changes in the Baltic Sea within the last 25 years*”, The 9th International Conference of the UNESCO Baltic Sea Project Science of Changes, Pirita SPA ja konverentsi hotell, Tallinn, Eesti 6.06.2015

- Stendiettekanne “*Factors affecting zebra mussel distribution on artificial substrate*“, Aquatic Science Meeting, ASLO, Granada, Hispaania 22–27.02.2015
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