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VELDA LAURINGSON

Role of suspension feeding in a brackish-water coastal sea

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Department of Zoology of the Institute of Ecology and Earth Sciences and Estonian Marine Institute, Faculty of Science and Technology, University of Tartu, Estonia

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Supervisor: Ph. D. Jonne Kotta, University of Tartu, Estonia

Opponent: Prof. Habil. Dr. Sergej Olenin, University of Klaipeda, Lithuania

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CONTRIBUTIONS

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Concept	VL, JK, +	VL, JK, +	JK	JK, VL, +	VL, JK
Design	JK, VL, +	JK, VL, +	JK, +	JK, +	VL, JK
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1. INTRODUCTION

The physical properties of water allow living creatures and particulate matter to remain in suspension, thereby creating a niche for suspension feeding – a widespread trophic strategy that does not occur on land. Suspension feeders capture, either actively or passively, tiny particles of food suspended in the water column. Such organisms can be roughly divided into two sub-groups: benthic and pelagic suspension feeders. Although exploiting the same food, the roles of these sub-groups in an ecosystem are in many ways controversial. Pelagic suspension feeders (PSF) recycle nutrients in the pelagial and make them to a great extent available for phytoplankton again (*e.g.* Jackson 1980, Viitasalo *et al.* 1999), while benthic suspension feeders (BSF) bring nutrients from the pelagic to the benthic system, therefore potentially suppressing further pelagic primary production and facilitating benthic primary production. Micro- and mesozooplankton are the most widespread representatives of PSF. These are small animals that have evolved mimicking their main prey, phytoplankton. They inhabit spatially the same area (water column) and follow temporally the ephemeral life cycle of their prey, multiplying quickly at the peak phase of phytoplankton. Doing so, their populations fluctuate in the same way as the populations of phytoplankton. BSF, on the other hand, are relatively long-lived and larger animals. They inhabit the seafloor and therefore depend on any kind of water movement bringing food-rich water close to their reach. In the marine environment, pelagic food webs are believed to prevail in open-sea areas, whereas benthic–pelagic coupling is generally more important in coastal sea areas and estuaries due to the short vertical distance between benthic and pelagic systems in shallow areas (Kautsky and Evans 1987, Kotta *et al.* 2008). The Baltic Sea represents a large and diverse estuarine habitat and BSF populations are widespread throughout the coastal range due to the absence of their main invertebrate predators in brackish-water conditions (Kautsky 1981, Reimer and Harms-Ringdahl 2001). It has been estimated that BSF are able to filter annually the total volume of the Baltic Sea (*e.g.* Kautsky and Kautsky 2000). Therefore, BSF are argued to have an important role in the energy flows of the Baltic Sea (Kautsky and Evans 1987, Kautsky and Kautsky 2000). In a shallow coastal sea, pelagic and benthic suspension feeders may co-exist. To date, the relative importance of either sub-group is very poorly studied. Although it is appropriate to study suspension feeders in a comprehensive framework, comparative studies of BSF and PSF are almost absent.

BSF can build up remarkably high biomasses in areas with a lush food supply. The amount of phytoplankton in the water is not the only important factor. Hydrodynamic energy enables BSF to reach the food. Therefore, large biomasses of BSF are almost always supported by frequent upwellings or riverine inputs of nutrients, together with tidal forces, strong wind-waves, or any other currents that constantly bring food-rich water to the vicinity of BSF. The vast majority of studies on BSF are conducted in such “energy replete” environments. However, low-energy systems also frequently occur in coastal areas. I use this term to refer to environments characterized by an absence of tidal forces, major upwellings, river inflows, and/or point sources of nutrients, and having usually flat coastal slopes. BSF are generally distributed sparsely in low-energy systems compared to nutrient replete areas with intense energy relocation processes.

The knowledge about the impact of BSF on benthic communities is centred around bivalve aquaculture in euhaline tidal seas (*e.g.* Mirto *et al.* 2000, Chamberlain *et al.* 2001, Crawford *et al.* 2003, Danovaro *et al.* 2004). Dense populations of BSF in aquaculture highly contrast the surrounding seafloor and are expected to influence the adjacent biota. Similarly, studies that examine BSF in natural habitats are almost exclusively focused on dense populations (*e.g.* Bertness 1984, Bracken 2004, Pfister 2007, Aquilino *et al.* 2009). There are virtually no examples from non-tidal low-energy systems.

In marine biology, the functional group approach is extremely common and often favoured over analysis involving the species level. The functional group level seems especially useful in large-scale descriptive analyses (Bonsdorff and Pearson 1999); conversely, in studies involving biotic interactions, the species level may be favourable (Posey 1990). The very small number of species in the Baltic Sea offers an excellent and rewarding opportunity to test the importance of species-specific traits within a studied functional group. Although different species of suspension feeders often co-exist in benthic communities, concurrent studies of the impact of different species of BSF are very uncommon to date.

Objectives

The objectives of the present thesis are (1) to evaluate the relative importance of BSF and PSF in the energy circuit of the coastal sea across naturally occurring environmental gradients in the characteristic low-energy ecosystems of the Northeastern Baltic Sea, and (2) to study the impact of energy flows generated by two common epifaunal BSF species at low natural densities on the adjacent biota in relation to the levels of exposure, eutrophication, and sediment type.

In BSF, an effort was made to detect species-specific traits. The response of the adjacent biota was analysed both at functional group and species levels (V).

The specific aims were to

(1) quantify and compare the grazing rates of benthic and pelagic suspension-feeder communities in a shallow coastal sea habitat, (I, II)
(2) relate differences in grazing rates to environmental conditions, (I, II)
(3) attempt to relate the coverage and biomass of the suspension-feeding cirriped *Balanus improvisus* Darwin to the coverage of the opportunistic macroalga *Ulva intestinalis* (L.), (III)
(4) evaluate the effect of the suspension-feeding mussel *Mytilus trossulus* Gould on macroalgal and associated invertebrate communities depending on the sediment type and exposure regime at different stages of annual succession, (IV)

(5) determine and compare the species-specific effects of the cirriped *Balanus improvisus* and the mussel *Mytilus trossulus* on macroalgal and associated epifaunal invertebrate communities at two different nutrient regimes. (V)

2. MATERIAL AND METHODS

2.1. Study area and organisms

The studies for the present thesis were conducted in the Northeastern Baltic Sea. The Baltic Sea is a semi-enclosed brackish waterbody, which lacks tidal cycles. Therefore, the intertidal habitat is missing. Owing to low salinity, only a few marine species manage to extend their distribution to this part of the sea. The freshwater species, however, are limited to even more diluted bays and estuaries (Kautsky and Kautsky 2000). The low diversity of communities and existence of organisms near their physiological tolerance limits make the ecosystem especially vulnerable to changes (Bonsdorff and Blomqvist 1993, Westerbom 2006). Although the summer temperature of the surface water can occasionally reach 28°C in some bays, usually temperatures fall below 20°C and in winter, an ice cover occurs, which may stay for over three months (Kotta *et al.* 2008). The Baltic Sea belongs to the most eutrophicated seas in the world due to the great anthropogenic input of nutrients coming from its large, densely populated drainage area (Wulff *et al.* 1990, Elmgren 2001). The sharp halocline causes a common lack of oxygen in deep waters at wide areas, leading to an accumulation of diluted phosphorus below the halocline (Nehring and Matthäus 1991). Phosphorus from deep water becomes available to biotic production through upwellings. The main upwelling regions are located at the western and northern coasts of the Baltic Proper, while the Northeastern Baltic Sea constitutes large downwelling areas (Myrberg and Andrejev 2003). The only exceptions are the northwestern coasts of the Väinameri and the Gulf of Riga; however, as both these basins are shallow with no permanent halocline, the effect of phosphorus-rich deep water on the development of coastal communities is weak compared to the upwelling regions of the Baltic Proper and the northern coast of the Gulf of Finland (Kotta *et al.* 2008).

Pelagic suspension feeders are dominated by a few species of copepods and rotifers supported by an autumn peak in meroplankton in open sea areas, while cladocerans and ciliates gain more importance in less exposed bays (Kotta *et al.* 2008). Dominant species are the copepods *Eurytemora affinis* (Poppe), *Acartia bifilosa* Giesb., and *Acartia tonsa* Dana, the cladocerans *Bosmina coregoni maritima* (PE Müller) and *Diaphanosoma brachyurum* (Lievin), the rotifers *Keratella quadrata* (Müller), *Synchaeta baltica* Ehrenberg, and *Brachionus quadridentatus* Hermann, and the ciliates from the genera *Strobilidium*, *Strombidium*, *Vorticella*, *Tintinnopsis*, *Mesodinium*, and *Didinium*. Meroplankton is dominated by larvae of the cirriped *Balanus improvisus* and a recent invader, the polychaete *Marenzelleria neglecta* Sikorski and Bick (Paper I). Both phyto- and zooplankton display strong seasonality, and suspension feeding activities are weak during winter. In abundance, copepods usually dominate in April and September, rotifers in May–August, and meroplankton in November, while in biomass, copepods dominate until the peak of meroplankton in November (Kotta *et al.* 2008). In the present study, the biomass of microzooplankton was higher at sheltered sites, and the biomass of mesozooplankton was higher at an exposed, eutrophicated site. Among microzooplankton, *Notholca* sp., *Strobilidium* sp., and *Vorticella* sp. were the most typical species in spring, *Keratella quadrata*, *Strobilidium* sp., *Synchaeta baltica*, and *Keratella cochlearis* (Gosse) in summer and *Strobilidium* sp. and *Strombidium* sp. in autumn. The species composition of mesozooplankton did not differ between seasons. I found no significant differences in the species composition of zooplankton at different sites; however, with a larger number of sites analysed, some differences may be revealed. The biomass of microzooplankton was negatively related to water salinity, the biomass of holoplanktonic mesozooplankton was positively related to water temperature and salinity, and the biomass of meroplankton was positively related to water chlorophyll (Chl *a*) content (I).

Three dominant epibenthic suspension-feeder species are studied in the present thesis: the bay mussel *Mytilus trossulus* (I, IV, V), the zebra mussel *Dreissena polymorpha* (Pallas) (I, II), and the bay barnacle *Balanus improvisus* (III, V).

Mytilus trossulus is a euryhaline marine intertidal species. In the Baltic Sea it displays some distinct features. Firstly, it remains notably smaller than in euhaline seas. Secondly, it inhabits from seashore down to over 30 m (Kautsky and Kautsky 2000). Salinity is considered to be the major limiting factor of the distribution of the bay mussel in the Baltic Sea (Westerbom 2006). The species is the most common benthic invertebrate species in the Baltic Sea area and is considered as highly important in the energy flows and ecosystem functioning (Kautsky and Evans 1987, Kautsky and Kautsky 2000). The species spreads mainly on rocky bottoms, gravel, and boulders, but also on soft bottoms, forming clumps or attaching to benthic vegetation. *Mytilus trossulus* is known to be abundant in areas where strong bottom currents and upwellings occur. The species has low densities in the less dynamic eastern part of the Baltic Proper. Although habitats with low mussel densities cover very large areas, to date they have remained virtually uninvestigated and the role of mussels unquantified (Kotta *et al.* 2005).

Dreissena polymorpha is often ranked as a freshwater species, although in its native habitats it inhabits areas from freshwater up to 5 psu (Shkorbatov *et al.* 1994). The species originates from the Ponto-Caspian region and is therefore more warmth-requiring than the other studied BSF species. *Dreissena polymorpha* was introduced to the Baltic Sea in 1824 (Thienemann 1950). Low temperatures and high salinities limit its distribution. In the Baltic Sea, the species is found at salinities below 6 psu with the highest biomasses in diluted estuaries (Järvekülg 1979, Olenin and Daunys 2005). In the Northern Baltic Sea, two areal centres exist: the less saline parts of the Gulf of Riga, as the main area of its distribution, and the eastern Gulf of Finland, where lower temperatures, however, seem to limit the species (Valovirta and Porkka 1996, Kotta *et al.* 1998). The species has not been found in the Väinameri (Kotta 2000). It may co-occur with *Mytilus trossulus*; however, in more diluted areas, the species seems to strongly dominate over the bay mussel (Kotta *et al.* 2008). The ecological role and importance of *Dreissena polymorpha* in the Baltic Sea are generally poorly understood, and evaluations are mainly based on distribution patterns.

Balanus improvisus is a suspension-feeding cirriped with a smaller body size than the bivalves described above. Although the species is widespread in the middle intertidal zone of euhaline seas all over the world, surprisingly little is known about the impact of the suspension-feeding activities of this species. *Balanus improvisus*, being a common fouling organism, is studied mostly from an economic point of view. The knowledge on the impact of the species on other biota is to a large extent limited to ecosystem engineering by structures that the calcareous shells of these animals provide. *Balanus improvisus* invaded the Baltic Sea in the late 19th century (Välikangas 1926). Today, the species is common all over the Baltic Sea, except the areas with the lowest salinity in the Bothnian Sea and Bothnian Bay and the eastern Gulf of Finland (Järvekülg 1979). *Balanus improvisus* inhabits hard bottoms from seashore down to 15 m and is among the first colonizers of new substrata or space cleared by ice scraping or other disturbances. At open rocky shores of the northern Baltic Proper, where epibenthic communities are characterized by the high biomass of bay mussels, a vigorous competition for space occurs, leaving barnacles outcompeted from primary substrata by mussels in the later stages of succession, although barnacles can continue growing attached to mussels (Laihonen and Furman 1986). In the less dynamic eastern Baltic Proper, space competition seems to be weaker, and mussels and barnacles often co-occur on cliffs, boulders, or bladderwrack. Moreover, in low salinity areas, barnacles may even oust mussels.

2.2. Experiments

This chapter briefly describes the methods that were used to fulfill the aims of the present thesis. More detailed descriptions of the methods are provided in the relevant papers.

My thesis consists of five experimental cycles. Two experimental cycles (Papers I and II) were run at four locations in the northern Gulf of Riga differing in salinity, exposure, and eutrophication level. The experiment described in Paper III was run in a semi-exposed Ihasalu Bay in the central Gulf of Finland and the experiment described in Paper V was run in a semi-enclosed bay of the inner archipelago in the middle of the Archipelago Sea, at the entrance to the Gulf of Finland (Figure 1). All experimental sites from papers I to IV represent characteristic low-energy systems. The experimental site in the

Archipelago Sea can be characterized as a low-energy system only at bay scale, as the outer Archipelago Sea experiences frequent upwelling events coupled with high hydrodynamic energy and therefore provides an energy-rich system. However, the enclosed bays of the Archipelago Sea represent a hydrologically different regime with much lower levels of water circulation compared to the outer Archipelago Sea.

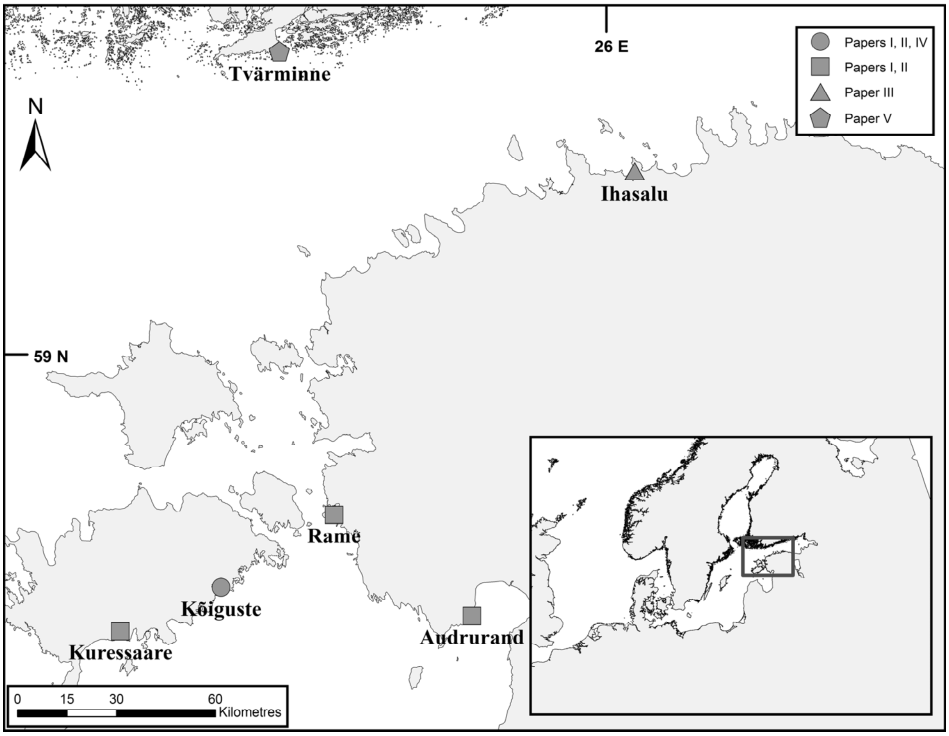

Figure 1. The experimental sites.

Pelagic and benthic grazing were compared at four sites to provide variability in salinity, exposure, and eutrophication (I). Biodeposition of BSF at specimen level and grazing by BSF and PSF at community level were related to ambient environmental conditions (I, II). These were short-term experiments and were replicated in spring, summer, and autumn in order to cover the annual growing period of phytoplankton. Other experiments were conducted to evaluate the impact of energy flows generated by benthic suspension feeding by bay mussels (IV, V) or barnacles (III, V) to benthic vegetation (III, IV, V) and macrofauna (IV, V). In more detail, these studies quantified the impact of barnacle feeding on the settlement and growth of the opportunistic macroalga *Ulva intestinalis* (III), the effects of sediment type, content of organic matter, exposure (IV), and eutrophication (V) on the responses to suspension feeding displayed by filamentous algae (IV, V), the charophyte *Chara aspera* Willdenow (IV), infauna (IV), and epifauna (IV, V). Exposure levels were set by choosing different locations while eutrophication levels were set by adding fertilizer to the experimental units. All these experiments were long-termed and lasted from June (III, IV) or July (V) to the end of September. In one experimental cycle, different successional stages were additionally sampled during summer (IV).

3. RESULTS AND DISCUSSION

3.1. Comparison of benthic and pelagic suspension feeding

The results showed that benthic suspension feeders remove much smaller amounts of phytoplankton biomass than pelagic suspension feeders in the study area, and both site and season affect the grazing rates (I, II). The grazing rates of BSF were related to site-specific environmental parameters and showed no relationship with water Chl *a* content whereas pelagic grazing rates were highly variable and increased with water Chl *a* content. On the other hand, the biodeposition of BSF was related to Chl *a* content. Mussel biodeposition initially increased with water Chl *a* content, but eventually levelled off at higher concentrations of food, indicating that both mussel species, *Mytilus trossulus* and *Dreissena polymorpha*, are unable to fully utilize the phytoplankton production of peak phases.

Several studies have suggested the high potential importance of benthic suspension feeding worldwide (*e.g.* Cloern 1982, MacIsaac *et al.* 1992) and likewise in the archipelago areas of the Northern Baltic Sea spatially close to my study area (Kautsky and Evans 1987, Kotta *et al.* 2005). Mesoscale variability in nearshore hydrography can determine the structure of benthic communities (Menge et al. 1997). Therefore, frequent upwellings in the northern and western parts of the Baltic Proper may be an important factor supporting high biomasses of BSF in these areas in contrast to the northeastern part of the Baltic Proper studied in the present thesis (I). Restricted food availability due to the benthic concentration boundary layer has been generally shown to limit the feeding of BSF (Fréchette *et al.* 1989, O'Riordan *et al.* 1995, Ackerman *et al.* 2001). Steep slopes can induce turbulent mixing in the bottom boundary layer (Slinn and Riley 1996), reducing near-bottom food limitation for BSF. Indeed, at steeper slopes, food seems not to be the limiting factor for the benthic communities (Kotta *et al.* 2007). The steep slopes characteristic of the rocky habitats of the Northern Baltic archipelago areas may, therefore, also account for the capacity of these areas to host noticeably larger biomasses of benthic suspension feeders than those recorded in my study area. BSF-driven energy fluxes play an important role in large river mouths in various parts of the Baltic Sea where low salinity allows *Dreissena polymorpha* to establish (Orlova *et al.* 2004, Kotta *et al.* 2005, Daunys *et al.* 2006) and the constant nutrient inflow helps to sustain much higher biomasses of mussels than in adjacent sea areas (Kotta *et al.* 2008). In contrast to these observations, my results indicate that in flat coastal habitats away from large rivers and upwelling areas, benthic suspension feeders play only a minor role in the foodweb dynamics, and pelagic processes strongly dominate over the benthic–pelagic coupling. Such habitats are widespread and typical of the Northeastern Baltic Sea and likewise in coastal areas of South Africa, and Arctic and Antarctic seas, to name just a few (Gutt 2001, Bownes and McQuaid 2006, Kotta *et al.* 2008). The sparsity of BSF at flat bottoms away from upwelling areas or riverine inputs may indicate food limitation as a primary structuring factor for BSF at flat bottoms.

In some studies, BSF have been shown to "control" the phytoplankton stock by their feeding activities, either keeping the abundance of phytoplankton constantly low (Cloern 1982) or causing abrupt shifts in the steady state of ecosystems previously devoid of dominant BSF communities after either new invasions or large increases in already existing species of BSF (Roberts 1990, Alpine and Cloern 1992, Petersen *et al.* 2008). In the Northeastern Baltic Sea, the dominant species of BSF have already quite a long invasion history (Leppäkoski and Olenin 2000); therefore, their populations currently constitute a part of a relatively mature ecosystem. The population sizes of BSF in the current study area seem to have adjusted very well to the low periods of phytoplankton biomass, described as "clearwater phases", while in the remaining periods they are unable to fully consume the high biomass of the peak phases of phytoplankton succession. The results suggest that in a flat non-tidal coastal habitat with neither direct riverine inputs nor recent shifts in ecological state, the pelagic recycling of energy is considerably higher than the amounts of energy directed from pelagic to benthic food-webs by BSF, and, thereby, BSF-driven energy flows likely play only a minor role in the pelagic food-web dynamics compared to pelagic processes.

3.2. Impact of benthic suspension feeding on the adjacent benthic biota

The present study indicates that BSF may have a significant effect on filamentous algae, charophytes, herbivores, and deposit feeders (III, IV, V). The main reason for the positive interaction with filamentous algae is likely an increased nutrient availability in the benthic system through the excretion and/or biodeposition by BSF (Reusch *et al.* 1994, Bracken 2004, Pfister 2007, Aquilino *et al.* 2009, III, IV, V). The growth of an algal canopy can be favoured by small-scale nutrient enrichment (Lotze *et al.* 2000, Bracken 2004). Additionally, the settlement of algae may depend on the qualities of the substrate. Some bacterial products, like homoserine lactones, have been shown to be especially attractive for the zoospores of *Ulva intestinalis* (Joint *et al.* 2002). As biodeposits of BSF may favour bacterial growth on adjacent substrata, the bacterial growth may subsequently attract zoospores of certain algae.

The direction of the impact of BSF varied among successional stages and organism groups (IV, V). The presence of *Mytilus trossulus* resulted in elevated biomasses of filamentous algae at the initial stages of algal succession (June, July) and in diminished biomass of charophytes at the later stages of algal succession (August, September), while the positive effect of *Mytilus trossulus* on herbivores was significant from July onwards (IV). It is plausible that *Mytilus trossulus* accelerates the growth of filamentous algae through the entire productive season, while, at the later stages of annual succession, the effect is likely counteracted by a heavy grazing pressure by mesoherbivores. This hypothesis is supported by a significantly higher biomass of grazers in treatments with BSF in later successional stages (IV, V). The presence of mussels resulted in the decline of charophytes at the later stages of annual succession. As shown earlier, mussels increase nutrient loads, leading to elevated productivity of ephemeral macroalgae. When charophytes are covered by filamentous algae, their photosynthetic activity presumably decreases and they become very attractive to herbivores (Kotta *et al.* 2004). Heavy grazing pressure on charophytes is expected given that there was a significantly higher grazer biomass in treatments with *Mytilus trossulus*.

Deposit feeders are often food limited in the temperate coastal marine ecosystems (Levinton and Stewart 1988*,* Ólafsson and Elmgren 1997*,* Kotta *et al.* 2001). BSF, on the other hand, are depositing noticeable amounts of energy-rich sediment on the seafloor in the form of faeces or pseudofaeces (Chamberlain *et al.* 2001, Norkko *et al.* 2001). My results agree with earlier evidence that the accumulation of faecal material induces elevated settlement and growth of deposit feeders (Dittmann 1990*,* Snelgrove and Butman 1994). Strong effects of mussels on deposit feeders were observed in the early stages of annual succession. At the later stages of annual succession, drift algae and their decomposition products provide an additional source of fresh detritus for deposit feeders (Lauringson and Kotta 2006, Kotta *et al.* 2008). This may explain the weak effects of mussels in this period. The author did not find any effect of suspension feeders on epifaunal deposit feeders in one experiment (V). In the design of this experiment, suspension feeders were attached on the top of the experimental units, mimicking their patchy occurrence on boulders. It can be assumed that the dissolved ammonia excreted by BSF was rapidly taken up by the adjacent flora while the deposits of suspension feeders were likely flushed away from the epifaunal communities by waves. If biodeposits are flushed away from the immediate vicinity of suspension feeders before being utilized by fauna, bacteria, or vegetation in natural communities, it seems possible to hypothesize that dissolved nutrients can account for the smaller scale patchiness while biodeposits can account for the larger scale patchiness in the distribution of benthic resources and biota around any excreting organisms.

Increased sedimentation in mussel beds can affect fauna in similar ways as any other organic enrichment, leading to decrease in faunal biomass (Commito and Dankers 2001). The switch from facilitation to suppression by BSF has been related to the increasing amount of suspended matter in the water column (Norkko *et al.* 2006). As suspended matter represents a form of bio-available energy, this finding is in good accordance with the results of the present study.

The lack of negative effects may be related to the low level of system-wide energy circulation, which leads to the paucity of BSF-mediated energy flows following the patchy, low-density distribution of suspension feeders.

Effects of exposure and sediment type

The interactive effect of *Mytilus trossulus* and exposure was significant only for macroalgae and not for benthic invertebrates. Stronger responses in macroalgal growth were observed in moderately exposed than in sheltered areas (IV). Except for phytoplankton blooms, the suspension-feeding bivalves are often limited by the availability of suspended particulate matter (Incze *et al.* 1981*,* Fréchette *et al.* 1989*,* Smaal *et al.* 2001), and increasing current velocity can reduce this limitation (Walne 1972*,* Fréchette and Bourget 1985). Indeed, the biodeposition activity of mussels was higher in exposed areas with high food availability compared to sheltered sites with low food availability (Kotta *et al.* 2005). Also, mussel population sizes are observed to be positively related to exposure (Westerbom and Jattu 2006). Westerbom and Jattu (2006) suggested higher sedimentation at less exposed sites as the cause for lower biomass, hypothesizing that a thin layer of muddy sediment on hard surfaces may develop more readily at less exposed sites and decrease the post-settlement success of mussel larvae. However, this causality is not fully proven yet. The results demonstrated here suggest that the mussels of the study area are limited by food access, which, in turn, depends on exposure.

The presence of *Mytilus trossulus* increased the biomass of deposit feeders on sand with a low content of organic matter but not on other substrate types (IV). Evidently, sediment composition may release deposit feeders from food limitation common in the area. Mussels also decreased the biomass of charophytes on sand with a low organic content to the values on organic-rich sediment. These results indicate that the organic content of the sediment may play an important role in modifying the outcome from biotic interactions and, specifically, from the nutrient-mediated impact of BSF.

Effect of nutrient addition

The background nutrient level generally affected biotic interactions in my study (V). The effect of suspension feeders did not override the effect of the added fertilizer but interacted with the latter, being usually weaker in fertilized treatments. In some cases, however, the impact of fertilizer and suspension feeder tended to cumulate. The large isopod grazer *Idotea balthica* (Pallas) was more promoted by suspension feeders at a high background nutrient level. This species has been shown to prefer filamentous algae as food (Orav-Kotta and Kotta 2004) and it probably profits from the higher production of algae in fertilized treatments. However, a lower production rate of algae and a lower biomass of the isopod co-occurred in both fertilized and unfertilized treatments with no suspension feeders. A possible explanation is a relatively fast diffusion of the nitrogenous component of the fertilizer used in the experiments, which may have caused nitrogen limitation for the benthic algae in all fertilized treatments. This limitation could have been easily alleviated by added suspension feeders, and the lush supply of phosphates in the fertilized treatments may have further promoted the observed higher production of filamentous algae and higher biomass of their main grazer in fertilized treatments with added suspension feeders compared to all other treatments. The situation may be similar in the Baltic Sea when phosphate-rich deep water enters shallow areas. The higher proportion of the small isopod *Jaera albifrons* Leach in unfertilized treatments may be connected to the preference of micro-scale food by this species (Sjöberg 1967). Filamentous algae are expected to be superior light competitors over benthic microalgae (McGlathery *et al.* 2001) and proliferate better in nutrient-rich conditions (Valiela *et al.* 1997); hence, food conditions may have been better for *Jaera albifrons* at a lower background nutrient level.

Species-specific effects

There are several studies on the impact of mussel-mediated energy input on benthic communities (*e.g.* Kautsky and Evans 1987*,* Pfister 2007*,* Aquilino *et al.* 2009), but contrastingly few similar studies involving barnacles (Williamson and Rees 1994). The author is to date not aware of any comparative studies on the impact of these organisms. Based on the present study, which revealed significant differences between the two species of BSF, the identity of BSF seems to be important in determining the response of benthic biota (V). The species composition and diversity of filamentous algae were distinctly affected by the addition of barnacles in the present study. This may be caused by several factors. The ability of algae to take up different nutritious substances may differ between taxonomic groups of algae (Bracken and Stachowicz 2006). Their ability to utilize nutrients may also depend on the dynamics of the nutrient supply (Pedersen and Borum 1997). Lotze and Schramm (2000), on the contrary, found the ecophysiological traits of two abundant taxa of our study, *Pilayella* and *Ulva*, to be relatively similar and hypothesized the distribution patterns of these species to be more influenced by ecological traits. Selective grazing pressure can be an important ecological factor limiting adult algae (Worm *et al.* 2000*,* Orav-Kotta and Kotta 2004) as well as modifying the settlement success of algal propagules (Korpinen *et al.* 2008). As the isopod *Jaera albifrons* is specialized mostly in microscale food items (Sjöberg 1967*,* Pavia *et al.* 1999), we can hypothesize that its greater abundance may have exerted selective pressure on algal settlement resulting in a more diverse canopy of adult algae in barnacle treatments. However, it is difficult to determine causalities based on my study, even if complex interactions, including the interactions between herbivores themselves, are left aside. For example, the higher diversity of algae in treatments with barnacles may have resulted (1) from the growth of bacteria possibly modified in barnacle treatments, which may induce selective attachment of zoospores of certain algae (Joint *et al.* 2002) or (2) from the grazing impact of *Jaera albifrons* either directly on the propagules of macroalgae or on the microalgal–bacterial biofilm, whose characteristics may be altered by the isopod grazing and may further alter the settlement success of algal species (Patel *et al.* 2003). High abundances of *Jaera albifrons* in treatments with barnacles may have, in turn, resulted from (1) more luxuriant growth of bacteria or microalgae (this hypothesis was not tested in the present study) or (2) a specific additional structure offered by barnacles, which may suit to certain zoobenthic taxa. However, the second reason is less likely, as barnacles were spatially separated from the epibenthic community that developed on the top of the bucket, and the isopod *Jaera albifrons* was favoured by barnacles exclusively in unfertilized treatments, which indicates a probability of a nutrient-linked factor to be involved.

The functional group approach treating the response of herbivores as a homogeneous group seems to neglect the large variability within the group in the ecosystem of the Northeastern Baltic Sea (V). I further categorized the group of herbivores based on mobility as mobile (mostly arthropods) and non-migratory (mostly snails) herbivores (Järvekülg 1979). Mobile arthropods were generally more favoured by suspension feeders than less mobile snails in my study; however, as also discussed above, responses of herbivore species to the presence of suspension feeders showed a significant interspecific variation.

Indirect effects

BSF increase algal biomass both in nutrient replete (Bracken 2004, Pfister 2007, Aquilino *et al.* 2009) and nutrient deplete systems (III, IV). The biomass of algae did not show any change in the vicinity of BSF in one experiment only (V). However, there was a clear increase in the ratio of herbivores to algal biomass, indicating higher production of algae in the vicinity of BSF in this experiment. Also, a concurrent decrease in charophytes and an increase in the biomass of herbivores in late successional stages of benthic communities were recorded in another experiment (IV). These findings suggest that macroalgal production was largely converted to herbivore biomass in the present study. Such bottom-up control is expected to prevail throughout several trophic levels and lead to a higher herbivore pressure in unproductive ecosystems compared to more productive ecosystems (Oksanen *et al.* 1981).

4. CONCLUSIONS

Benthic suspension feeders graze a much smaller part of the pelagic primary production than pelagic suspension feeders in flat coastal areas with low hydrodynamic energy and no direct nutrient inputs, referred to as “low-energy systems” in the present thesis. Consequently, BSF seem likely to have only a marginal role in the pelagic energy circuit in such areas (I). However, and despite their sparse distribution, BSF have an important role in structuring benthic communities in low-energy systems (III, IV, V). The outcome from interactions between BSF and the adjacent biota depends on site-specific parameters like exposure, sediment type, and background nutrient level (IV, V). The impact of grazing by individual mussels on the development of benthic communities is stronger at higher exposure (IV). As grazing by communities of BSF tended to increase with exposure (I), the structuring impact of a community of BSF on the adjacent benthic biota in a low-energy system is supposedly even more related to exposure than that of individual mussels. These findings may hint that BSF are hydrodynamically limited in their access to food in the study area and underline the importance of exposure as one of the key factors in structuring benthic communities in the shallow coastal sea.

The outcome from interactions between BSF and the adjacent biota in low-energy systems resembles nutrient replete areas in that benthic macrovegetation is promoted by BSF (III, IV, V). Distinct features may be the lack of detrimental effects on the deposit-feeder community (IV) and a frequent facilitation of herbivores (IV, V). The latter may hint bottom-up control as a prevailing type of limitation for herbivores in such low-energy systems. As energetic limitation seems common in both herbivores and deposit feeders in the study area (IV, V), the ecosystem at low-energy areas may be especially sensitive to any shift in the energy circuit generated by BSF. Species-specific traits in interactions between BSF and the adjacent biota were well distinguishable in the present study (V). These findings emphasize the potential ecological importance of even small changes in species distributions, as a slight increase in a certain species of BSF in a susceptible ecosystem could possibly release some previously limited species or group of species and lead to unexpected cascading effects via subsequent changes in several trophic levels.

SUMMARY

Suspension feeding is an extremely widespread feeding strategy in aquatic animals and, supposedly, constitutes a highly important part of ecosystem processes in marine and limnic systems. Suspension-feeding organisms can be divided into two major groups: benthic and pelagic suspension feeders. The majority of benthic suspension feeders (BSF) are relatively long-lived animals with low mobilty, therefore depending on hydrodynamic forces in their supply of food. Pelagic suspension feeders (PSF) are usually small and short-lived, following their phytoplankton prey both in space and time. The ecological roles of BSF and PSF also differ: PSF recycle nutrients mostly in the pelagic system, facilitating pelagic production, while BSF can redirect nutrients from the pelagic to the benthic system in shallow sea areas and facilitate benthic production, both at primary and at secondary level.

The aim of the present thesis was to study the relative importance of benthic and pelagic suspension feeding in low-energy systems, i.e. in areas with relatively poor energy supplies as opposed to high-energy systems with lush supplies of energy through upwellings, intense hydrodynamic forces, or local nutrient inputs. Most of the studies on BSF are conducted in energy replete environments that support high biomasses of BSF. In contrast, the distribution of BSF is sparse in the low-energy system.

Five field experiments were conducted in the shallow coastal Norheastern Baltic Sea to compare the grazing rates of BSF and PSF under different short-term (temperature, salinity, water Chl *a* content) and long-term (eutrophication, exposure) environmental conditions (I, II) and to measure the impact of BSF-mediated energy flows on benthic communities (III, IV, V). The impact was analysed both at functional group and at species level (V). A separate field survey was conducted to assess the population sizes of BSF and PSF (I).

Although temperature, salinity, and water Chl *a* content were all important factors in determining the biodeposition rate of individual BSF (I, II), the grazing rate of the BSF community appeared to be related only to site-specific long-term environmental factors (I). The grazing rate of the PSF community was, in contrast, related to both long-term factors and short-term Chl *a* content of the water (I).

In low-energy areas, BSF grazed a much smaller part of the pelagic primary production than PSF. Consequently, BSF seem likely to have only a marginal role in the pelagic energy circuit in such areas (I). However, and despite their sparse distribution, BSF had an important role in structuring benthic communities in low-energy systems (III, IV, V). The outcome from interactions between BSF and the adjacent biota depended on site-specific parameters like exposure, sediment type, and background nutrient level (IV, V). Species-specific traits were well distinguishable (V).

In the studied low-energy system, the impact of BSF-mediated energy flows on the adjacent biota resembled energy replete areas in that benthic macrovegetation was promoted by BSF (III, IV, V). The most noticeable distinct feature was a frequent facilitation of herbivores (IV, V). Such a vigorous conversion of plant biomass to the next trophic level may hint bottom-up control as a prevailing type of limitation for herbivores in a low-energy system. Deposit feeders also seemed to profit from BSF-mediated energy flows on nutrient-poor sediments in the study area (IV).

The results suggest a significant impact of BSF on benthic communities in an ecosystem with a low energy input despite the sparsity of BSF in such a habitat and apparent low biomasses and energy flows involved in benthic–pelagic coupling processes. Benthic communities in low-energy areas may be especially sensitive to a shift in the energy circuit generated by BSF. BSF are likely hydrodynamically limited in their access to food in the study area, underlining the importance of exposure as one of the key factors in structuring benthic communities in the shallow coastal sea. High interspecific variation in biotic interactions emphasizes the potential ecological importance of even small changes in species distributions.

SUMMARY IN ESTONIAN

Hõljumtoiduliste organismide tähtsus riimveelises rannikumeres

Hõljumi filtreerimine on veeloomade seas erakordselt laialt levinud toitumisstrateegia ning moodustab olulise osa mere- ja järveökosüsteemide ökoloogilistest protsessidest. Hõljumtoidulisi organisme saab jagada kahte suurde rühma: bentilised ehk põhjaeluviisiga ja pelaagilised ehk veemassi asustavad filtreerijad. Bentilised filtreerijad (BF) on enamasti suhteliselt pika eluea ja paigalise eluviisiga loomad, kelle jaoks toidu kättesaadavus sõltub vee liikumisest. Pelaagilised filtreerijad (PF) on tavaliselt väikesed ja lühikese elueaga nagu nende fütoplanktonist saakobjektidki. Ka PF ja BF ökoloogilised rollid on erinevad – PF töötlevad toitaineid veemassis ümber ja soodustavad seeläbi pelaagilist produktsiooni, kuna BF võivad madalatel merealadel suunata toitaineid veemassist põhjakooslustesse, soodustades bentilist produktsiooni.

Doktoritöö eesmärgiks oli uurida BF ja PF tähtsust energiavaestes süsteemides. Sellised süsteemid esinevad merealadel, kus energia ümberpaigutumisega seotud protsessid, näiteks süvavee kerked, hoovused, tõusu- või tuulelained ja vooluvete sissevool, on nõrgad. Enamik uurimusi BF kohta on läbi viidud energiarikastes süsteemides, mida samuti iseloomustab ka suur BF biomass. Energiavaestes süsteemides on BF seevastu hõreda levikuga ja väheuuritud. BF ja PF võrdlevad uuringud senini praktiliselt puuduvad.

Uurimuse raames viidi Läänemere kirdeosa madalas rannikumeres läbi viis välikatset. Lühiajaliste katsete käigus uuriti vee temperatuuri, soolsuse ja klorofüll *a* sisalduse mõju filtreerijate toitumisele ning võrreldi BF ja PF osakaalu erineva toitelisuse ja avatusega aladel (I, II). Pikaajaliste katsete käigus uuriti toitelisuse, avatuse ja sette tüübi mõju BF poolt tekitatud energiavoogudele (III, IV, V). Analüüsiti BF mõju nii toitumisrühma kui liigi tasandil (V). Välitöödel hinnati ka BF ja PF populatsioonide suurust rannikumeres (I).

Katsetest selgus, et ehkki vee temperatuur, soolsus ja klorofüllisisaldus mõjutasid oluliselt BF toitumist üksikisendi tasemel (I, II), on BF koosluse toitumine seotud ainult asukohast sõltuvate, ajas suhteliselt stabiilsete keskkonnatingimustega – piirkonna avatuse ja toitelisusega (I). Seevastu PF koosluste toitumine oli seotud nii piirkonna avatuse ja toitelisusega kui ka vee klorofüllisisaldusega (I).

Uuritud merepiirkondades eemaldasid PF veemassist palju rohkem fütoplanktonit kui BF. Sellest tulenevalt võib oletada, et energiavaestel aladel on BF roll pelaagilises energiaringes tühine (I). Ometi mõjutasid BF hoolimata hõredast asustustihedusest oluliselt põhjakoosluste koosseisu (III, IV, V). BF mõju ümbritsevale elustikule sõltus piirkonna avatusest, toitelisusest ja sette tüübist (IV, V). Liigiomased erinevused olid hästimärgatavad (V).

Sarnaselt energiarikastele merealadele soodustas BF vahendatud energiavoog suurvetikate kasvu ka uuritud energiavaestel aladel (III, IV, V). Tähelepanuväärseimaks erisuseks oli BF sageli esinev soodne mõju herbivooridele energiavaestes süsteemides (IV, V). Sedavõrd intensiivne taimse biomassi ülekanne järgmisele toitumistasandile võib viidata valdavalt alt-üles (*bottom-up*) suunatud kontrollmehhanismidele herbivooride arvukuse reguleerimisel energiavaestes süsteemides. Uurimisala toitainevaesematel setetel soodustas BF poolt vahendatud energiavoog ka detrivooride arengut.

Doktoritöö tulemused viitavad BF vahendatud energiavoo suurele tähtsusele energiavaeste rannikumerealade põhjakoosluste kujundajana, seda hoolimata BF hõredast levikust ning nendega seotud energiavoo väikesest osakaalust uuritud ökosüsteemide energiaringes. On võimalik, et BF poolt põhjustatud muutused energiaringes mõjutavad eriti tugevalt just energiavaeste alade põhjakooslusi. Kuna tõenäoliselt piirab vee liikuvus oluliselt BF arvukust ja toitumist uuritaval alal, võib seega järeldada, et piirkonna avatusel on madalmere põhjakoosluste kujunemisel tähtis roll. Koosluste toimimisele võib märgatavat mõju avaldada ka BF liigiline koosseis – muutused ühe liigi levilas võivad kaasa tuua ulatuslikke tagajärgi erinevatel toitumistasanditel ja mõjutada rannikumere ökosüsteemi kui tervikut.

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PUBLICATIONS

CURRICULUM VITAE

I. General

Name:	Velda Lauringson
Date and place of birth:	30.09.1975 Tallinn
Citizenship:	Estonian
Address, e-mail:	Mäealuse 10a, 12618 Tallinn, Estonia, velda.lauringson@ut.ee
Position:	Estonian Marine Institute, University of Tartu, researcher
Educational history:	M.Sc., Hydrobiology, University of Tartu, 2005 B.Sc., Hydrobiology, University of Tartu, 2003 Tallinn Lilleküla High School, 1993 Tallinn Secondary School No. 44, 1990
Languages spoken:	Estonian, English, Finnish
Professional employment:	Researcher, Estonian Marine Institute, University of Tartu, since 2005 Technician, Estonian Marine Institute, University of Tartu, 2003–2005

II. Research History

Research interests

The role of suspension feeders in the coastal sea ecosystem; the impact of eutrophication on benthic communities

Peer-reviewed publications

1. Lauringson V., Kotta J., Orav-Kotta H., Kotta I., Herkül K., Põllumäe A. (2009) Comparison of benthic and pelagic suspension feeding in shallow water habitats of the northeastern Baltic Sea. *Marine Ecology*, **30**, 43–55.
2. Veber T., Kotta J., Lauringson V., Kotta I. (2009) Influence of the local abiotic environment, weather and regional nutrient loading on macrobenthic invertebrate feeding groups in a shallow brackish water ecosystem. *Oceanologia*, **51**, 541–559.
3. Kotta J., Lauringson V., Martin G., Simm M., Kotta I., Herkül K., Ojaveer H. (2008) Gulf of Riga and Pärnu Bay. In: Schiewer, U. (Ed.). *Ecology of Baltic Coastal waters. Ecological Studies, Vol. 197.* Springer, Berlin/ Heidelberg: 217–243.
4. Kotta J., Lauringson V., Kotta I. (2007) Response of zoobenthic communities to changing eutrophication in the northern Baltic Sea. *Hydrobiologia*, **580**, 97–108.

5. Lauringson V., Mälton E., Kotta J., Kangur K., Orav-Kotta H., Kotta I. (2007) Environmental factors influencing the biodeposition of the suspension feeding bivalve *Dreissena polymorpha* (Pallas): comparison of brackish and fresh water population. *Estuarine, Coastal and Shelf Science*, **75**, 459–467.
6. Kotta J., Kotta I., Simm M., Lankov A., Lauringson V., Põllumäe A., Ojaveer H. (2006) Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Marine Research*, **60**, 106–112.
7. Lauringson V., Kotta J. (2006) Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. *Hydrobiologia*, **554**, 97–105.

Grants and Scholarships

2009	Archimedes Foundation, Kristjan Jaak travel grant
2008	Archimedes Foundation, Kristjan Jaak travel grant
2007	Doctoral School of Ecology and Environmental Sciences, funding for PADI Open Water Diver Course
2004	CIMO (Center for International Mobility) scholarship for research in the Tvärminne Zoological Station, University of Helsinki, Finland
2004	Estonian Students' Fund, Mathiesen Scholarship

Conferences

Lauringson V, Kotta J. „Effects of suspension feeding mussel *Mytilus trossulus* and barnacle *Balanus improvisus* on brackish water benthic communities.“ 44th European Marine Biology Symposium, 7–11. 09. 2009, Liverpool, Great Britain. (presentation)

Kotta J, Orav-Kotta H, Lauringson V, Kaljurand K, Kotta I. „Food items of bivalve suspension feeders in the NE Baltic Sea.“ 7th Baltic Sea Science Congress, 17–21. 08. 2009, Tallinn, Estonia. (presentation)

Kotta J, Herkül K, Kotta I, Orav-Kotta H, Lauringson V. „Scale dependent effects of the suspension feeding mussel *Mytilus trossulus* on macroalgal and associated invertebrate assemblages.” 43rd European Marine Biology Symposium, 8–12. 09. 2008, Ponta Delgada, Portugal. (presentation)

Lauringson V, Kotta J, Orav-Kotta H, Kotta I, Herkül K. „Grazing by benthic and pelagic suspension feeders in a shallow coastal sea ecosystem.” 43rd European Marine Biology Symposium, 8–12. 09. 2008, Ponta Delgada, Portugal. (presentation)

Veber T, Kotta J, Lauringson V, Kotta I. „Role of coastal geomorphology modulating the relationships between climate, eutrophication variables and benthic invertebrate communities.” 43rd European Marine Biology Symposium, 8–12. 09. 2008, Ponta Delgada, Portugal. (poster)

Kotta J, Orav-Kotta H, Lauringson V, Kaljurand K, Kotta I. „Do benthic suspension feeders feed selectively on diatom species in the shallow coastal ecosystem of the Baltic Sea?” 42nd European Marine Biology Symposium, 27–31. 08. 2007, Kiel, Germany. (presentation)

Lauringson V, Kotta J, Kangur K, Orav-Kotta H, Herkül K, Kotta I. „The feeding activity and invasibility of *Dreissena polymorpha*: comparison of brackish and fresh water populations.” Evolutionary Conservation Biology Workshop, 11–14. 10. 2005, Häädemeeste, Estonia. (poster)

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Kotta J, Lauringson V, Kotta I. „Role of functional diversity and physical environment on the response of zoobenthos communities to changing eutrophication.“ 39th European Marine Biology Symposium, 21–24. 07. 2004, Genova, Italy. (presentation)

CURRICULUM VITAE

I. Üldandmed

Ees- ja perekonnanimi: Velda Lauringson
Sünniaeg ja koht: 30.09.1975 Tallinn
Kodakondsus: eesti
Aadress, e-post: Mäealuse 10a, 12618 Tallinn, Eesti,
velda.lauringson@ut.ee
Praegune töökoht, amet: TÜ Eesti Mereinstituut, teadur
Haridus: M.Sc. hüdrobioloogias, Tartu Ülikool, 2005
B.Sc. hüdrobioloogias, Tartu Ülikool, 2003
Tallinna Lilleküla Keskkool, 1993
Tallinna 44. Keskkool, 1990
Keelteoskus: eesti, inglise, soome
Teenistuskäik: Teadur, Eesti Mereinstituut, Loodus- ja tehnoloogiateaduskond, Tartu Ülikool, alates 2005
Laborant, Eesti Mereinstituut, Loodus- ja tehnoloogiateaduskond, Tartu Ülikool, 2003–2005

II. Teaduslik ja arendustegevus

Peamised uurimisvaldkonnad

Hõljumisööjate tähtsus rannikumere ökosüsteemis, eutrofeerumise mõju mere põhjaloomastikule

Publikatsioonid rahvusvahelise levikuga väljaannetes

1. Lauringson V., Kotta J., Orav-Kotta H., Kotta I., Herkül K., Põllumäe A. (2009) Comparison of benthic and pelagic suspension feeding in shallow water habitats of the northeastern Baltic Sea. *Marine Ecology*, **30**, 43–55.
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Saadud uurimistoetused ja stipendiumid

2009	SA Archimedes, Kristjan Jaagu välissõidu stipendium
2008	SA Archimedes, Kristjan Jaagu välissõidu stipendium
2007	Ökoloogia ja keskkonnateaduste doktorikool, PADI OWD sukeldumiskursuse rahastus
2004	CIMO (Center for International Mobility), stipendium uurimistööks Helsinki Ülikooli Tvärminne Zooloogiajaamas Soomes
2004	Eesti Üliõpilaste Toetusfond, Mathieseni nimeline stipendium

Konverentside ettekanded

Lauringson V, Kotta J. „Effects of suspension feeding mussel *Mytilus trossulus* and barnacle *Balanus improvisus* on brackish water benthic communities.“ 44th European Marine Biology Symposium, 7–11. 09. 2009, Liverpool, Suurbritannia. (ettekanne)

Kotta J, Orav-Kotta H, Lauringson V, Kaljurand K, Kotta I. „Food items of bivalve suspension feeders in the NE Baltic Sea.“ 7th Baltic Sea Science Congress, 17–21. 08. 2009, Tallinn, Eesti. (ettekanne)

Kotta J, Herkül K, Kotta I, Orav-Kotta H, Lauringson V. „Scale dependent effects of the suspension feeding mussel *Mytilus trossulus* on macroalgal and associated invertebrate assemblages.” 43rd European Marine Biology Symposium, 8–12. 09. 2008, Ponta Delgada, Portugal. (ettekanne)

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