ORIGINAL ARTICLE

Comparison of benthic and pelagic suspension feeding in shallow water habitats of the Northeastern Baltic Sea

Velda Lauringson[1,2], Jonne Kotta[1], Helen Orav-Kotta[1], Ilmar Kotta[1], Kristjan Herkül[1,2] & Arno Põllumäe[1]

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

Abstract

Combining field experiments with the biomass distribution data of dominant suspension feeders we compared the benthic and pelagic suspension feeding rates in shallow non-tidal brackish water coastal habitats. We found that pelagic grazing exceeded benthic grazing in almost all cases, on average from 14 to 4819 times depending on the site. Benthic grazing rates were related to site-specific environmental parameters and showed no relationship with water chlorophyl a (Chl a) content, whereas pelagic grazing rates varied both spatially and temporally and were related to water Chl a content. Our results indicate that in several shallow coastal habitats, pelagic suspension feeding substantially exceeds benthic suspension feeding. This suggests that pelagic recycling is higher than the amounts of energy redirected from pelagic to benthic food webs by benthic suspension feeders. These results increase our knowledge of the energy flows in coastal ecosystems.

Problem

Suspension feeding mode is 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 organisms with low mobility, characterized by high spatial variability but temporal stability (Kotta *et al.* 2005). Conversely, most pelagic suspension feeders (PSF), being short-lived and able to quickly spread over long distances, are characterized by high temporal variability and spatial stability (Lundberg & Moberg 2003).

Although benthic and pelagic suspension feeders exploit the same food, they have quite different roles in food webs. Whereas PSF recycle a large share of the nutrients in the water column (Viitasalo *et al.* 1999), making them again quickly available to phytoplankton and facili-

tating phytoplankton growth (Jackson 1980), this is not always the case for BSF, which are often shown to redirect a large share of nutrients from the pelagic to the benthic system (Reusch *et al.* 1994; Norkko *et al.* 2001; Norling & Kautsky 2007). BSF have therefore been considered a natural eutrophication control, especially in turbid, nutrient-replete systems (Cloern 1982; Officer *et al.* 1982; Kautsky & Evans 1987). 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 & 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 predators in brackish-water conditions. Therefore, BSF are believed to have an important role in the energy flows of the Baltic
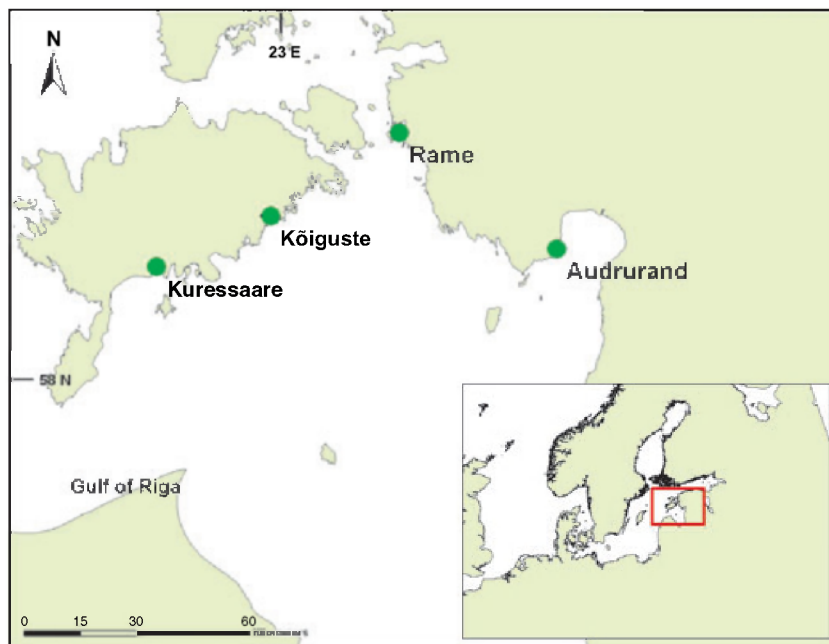
Fig. 1. The study area. Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.

Sea (Kautsky & Evans 1987; Kautsky 1995). Locally, dense populations of BSF are capable of clearing the overlying water column 20 times daily and BSF patchiness is considered to process about 90% of the phytoplankton stock in the coastal range of the Baltic Sea (Kotta & Møhlenberg 2002; Kotta *et al.* 2005). In such habitats PSF, namely mesozooplankton, are scarce and they are considered to have a marginal role in the energy flows (Kotta *et al.* 2008). PSF in marine and estuarine environments have seldom been studied as a functional group and their role in and impact on ecosystems are mainly speculative (Bushek & Allen 2005). A number of studies have been published separately on both benthic and pelagic grazing for a wide range of water-bodies. Despite the fact that these two feeding modes are exploiting the same food, comparative studies that experimentally evaluate benthic and pelagic grazing are rare and are almost absent for estuarine ecosystems. The subject is essential to improve our understanding about the roles that different functional groups play in coastal ecosystem functioning.

The aim of our study is to compare the grazing rates of benthic and pelagic suspension-feeding modes in a temperate non-tidal brackish coastal sea. We tested whether benthic grazing on phytoplankton prevails over pelagic grazing in different shallow water habitats and how local environmental conditions modify the grazing rates. Our experimental observations covered the main growing seasons of phytoplankton as well as small hydrodynamic, eutrophication and salinity gradients naturally occurring in the area. We assumed that (i) grazing by BSF is higher than grazing by PSF in shallow coastal areas

and (ii) different environmental variables modify the relative contribution of benthic and pelagic grazing.

Study Area

The study area is a non-tidal, brackish-water ecosystem located in the Northeastern Baltic Sea (Fig. 1). We chose four study sites in the Gulf of Riga covering local gradients in exposure, eutrophication and salinity: Audrurand represents an exposed eutrophic site, Kuressaare a sheltered eutrophic site, Kõiguste an exposed mesotrophic site, and Rame a sheltered mesotrophic site. The sites have flat-bottom topography. A mixture of pebbles, sand and silt characterizes the studied sites with a higher proportion of silty sediments in eutrophic sites. All sites were located away from large riverine loads or upwelling areas. Salinity varied between 1.5 and 5, temperature was 12–28 °C, water velocity 0–20 cm·s^{-1}, and water chlorophyll *a* (Chl *a*) content 3.6–56 mg·m^{-3} (Table 1).

Material and Methods

Benthic and pelagic grazing was experimentally evaluated at 1 m depth at each study site in spring, summer and autumn 2003. The two dominant benthic suspension feeders *Mytilus trossulus* Gould and *Dreissena polymorpha* (Pallas) were collected from the Audrurand and Kõiguste sites and allowed to adapt to the ambient conditions for 12 h before the start of the experiment. Three mussels were placed on a net with a mesh size of 1 cm. The mesh was glued on the top of a solid funnel (diameter 8 cm,

Table 1. Environmental factors, biomasses of different ecosystem elements and pelagic primary production by different sites and seasons.

Site/season	T	S	Velocity	Chl a	PP	MesoZP	MeroP	MicroZP	Mussels Mytilus	Dreissena
Audrurand										
spring	14.7	3.8	10.1 ± 26.3	18 ± 1	0.45 ± 0.10	13 ± 10	2 ± 1	1411 ± 170	71 ± 112	14571 ± 8889
summer	28.1	4.2	0.0 ± 0.0	21 ± 16	*0.00	219 ± 201	28 ± 12	574 ± 120	107 ± 161	20000 ± 8346
autumn	14.3	4.6	2.7 ± 3.0	56 ± 16	0.80 ± 0.42	26 ± 22	501 ± 102	112 ± 98	107 ± 151	21786 ± 8415
Kuressaare										
spring	13.8	2.0	2.3 ± 2.3	21 ± 5	0.21 ± 0.18	39 ± 33	69 ± 34	2731 ± 73	54 ± 10	0
summer	22.7	1.5	4.3 ± 10.7	8 ± 0	0.19 ± 0.08	11 ± 7	0	3107 ± 65	71 ± 21	0
autumn	11.9	4.1	1.1 ± 0.7	44 ± 0	0.49 ± 0.30	13 ± 6	0	2317 ± 103	89 ± 14	0
Kõiguste										
spring	14.7	3.8	0.0 ± 0.0	4 ± 1	0.09 ± 0.06	5 ± 2	0	333 ± 153	3250 ± 1234	0
summer	25.6	4.5	6.7 ± 14.4	4 ± 1	0.09 ± 0.08	24 ± 21	0	899 ± 147	3964 ± 2499	0
autumn	13.2	4.7	20.4 ± 76.3	14 ± 9	0.25 ± 0.16	19 ± 17	0	88 ± 75	4286 ± 3865	0
Rame										
spring	14.5	2.5	2.9 ± 2.6	9 ± 1	0.13 ± 0.12	42 ± 33	0	2730 ± 104	3975 ± 3294	0
summer	27.2	4.9	1.0 ± 0.3	11 ± 6	0.44 ± 0.28	139 ± 100	3 ± 1	1323 ± 131	4500 ± 1898	0
autumn	12.8	4.7	0.0 ± 0.0	5 ± 1	0.12 ± 0.09	15 ± 11	0	1795 ± 125	5500 ± 3482	0

T = temperature (°C); S = salinity (psu); Velocity = water current speed (cm·s^{-1}); Chl a = water chlorophyll a (mg·m^{-3}); PP = phytoplankton primary production (mg Chl a h^{-1}·m^{-3}); MesoZP = mesozooplankton biomass (mg wet weight m^{-3}); MeroP = meroplankton biomass (mg wet weight m^{-3}); MicroZP – microzooplankton biomass (mg wet weight m^{-3}); Mussels = biomass of Mytilus trossulus and Dreissena polymorpha (mg dry weight m^{-2}).
'±' SE values; '*' phytoplankton decomposition exceeded primary production values.

height 5 cm) allowing biodeposits to sediment into the collecting vial below. The unit was located on the sediment surface, and was similar in size to the dimensions of boulders in the study area (Kotta & Møhlenberg 2002). As the mussels were deployed on the top of the unit and there were no structures separating the mussels and the ambient water, it is likely that the bivalves were exposed to the same amount of phytoplankton as measured in the ambient water column. Each incubation lasted 4 h. In every season we performed at least five incubations with three concurrent replicates. Water temperature and salinity were monitored at the beginning and at the end of each experiment using CTD profiling. Salinity was measured using the Practical Salinity Scale. Current velocity was measured every second using a calibrated electromagnetic current recorder connected to a data logger (Compact-EM data recorder by Alec Electronics). After deployment, the shell lengths of mussels were recorded, and the sedimented material from the vials was sorted under a dissecting microscope. Faeces were collected with a pipette and filtered on Whatman CF/F filters within 4 h of retrieval. Filters were extracted in the dark with 96% ethanol overnight. Chl a was quantified spectrophotometrically correcting for phaeopigments (Pha a) (Strickland & Parsons 1972). The values of Chl a equivalent or total Chl a (Chl a eq) were calculated as Chl a eq = Chl a + 1.52 × Pha a. Pseudofaeces production was uncommon at studied sites and times. During deploy-

ment, water for Chl a measurement was sampled every 4 h by a diver at near-bottom layer, 25 cm from the cages. On each occasion, 2 liters of water was sampled three times and filtered on Whatman CF/F filters within 4 h of retrieval. Further processing of samples followed the procedures described above.

To estimate loss of Chl a in the digestive tract, separate experiments were carried out on land. Mussels were incubated in 5-liter buckets filled with natural seawater for 4 h. In each bucket, five mussels were used; buckets without experimental animals served as controls. At the end of incubation, biodeposits were collected from the buckets by careful pipetting and water samples for Chl a were taken. The content of Chl a and Pha a was estimated in biodeposits and water samples as described above. The loss of Chl a during gut passage was estimated as the ratio of the loss of Chl a in water to biodeposit production, taking into account algal growth and sedimentation in the control bucket. Functional relations between biodeposition and environmental variables were determined after correction for loss of Chl a during gut passage. The loss of Chl a during digestion by BSF did not exceed 20% and was usually estimated at less than 10% (Fig. 2). Grazing by individuals of different sizes (G_l) was scaled by shell length, i.e. $G_l = G_{20} \times l^2/20^2$, where G_{20} is the grazing rate of 20 mm individuals and l the shell length (Kiørboe & Møhlenberg 1981). Biodeposition rate of mussels was expressed as the amount of Chl a and phaeopigments digested by a 20-mm
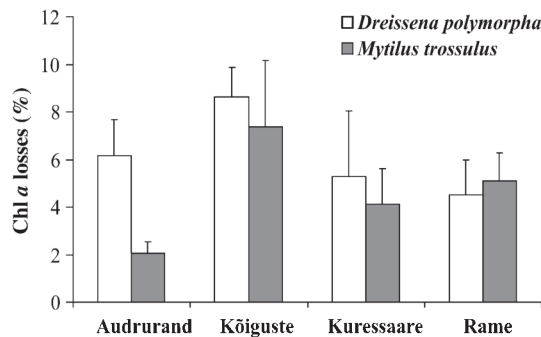
Fig. 2. Estimates of loss of Chl *a* in the digestive tract of bivalves at different sites.

bivalve in 1 h, adjusted for Chl *a* loss in the digestive tract (Lauringson *et al.* 2007).

Pelagic suspension feeding was evaluated in 15-liter plastic bags filled with seawater consisting of natural phytoplankton and zooplankton communities. Control bags were filled with water sieved through a 55-μm net to remove most of the zooplankton and were kept in transparent (photosynthetic production experiments) or dark plastic bags (dark respiration experiments). Chl *a* samples were taken at the beginning of the experiment and after 2 and 5 h of deployment. Plastic bags were suspended in the upper 0.5 m of the water column and incubated simultaneously with benthic grazing experiments. At the end of the experiment all water was filtered through Whatman CF/F filters and processed in the same way as other water samples described above. Changes in Chl *a* over the experiment in the transparent control bag were used as a proxy of net photosynthetic production of phytoplankton. Changes in Chl *a* in the dark control bag gave us an estimate of the decomposition of phytoplankton. Pelagic grazing was assessed as the amount of Chl *a* removed in the transparent plastic bag containing zooplankton, adjusted for Chl *a* production and losses in the control experiment.

Filtration and extraction of water samples for Chl *a* measurement were carried out within 1 h after sampling. The samples were filtered onto Whatman GF/F filters. Chl *a* and Pha *a* were measured as noted above. In every site and season, additional water samples were taken to determine the species composition of phytoplankton. These samples were preserved in acid Lugol solution and counted under an inverted microscope. Wet weight of different species was calculated from cell geometry (HELCOM 1988). We were not able to determine phytoplankton species composition in autumn samples due to the very high turbidity of these samples.

To determine the time-scale of the fluctuations in food abundance for suspension feeders, water Chl *a* content

was recorded every second using the calibrated chlorophyll/turbidity recorder connected to a data logger (Compact-CLW data recorder by Alec Electronics) at Kõiguste site during the ice-free seasons of 2003. The temporal patterns of phytoplankton are known to be similar in all four locations studied, although there are differences in the peak values due to their different eutrophication levels (Kotta *et al.* 2008).

During experiments the size structure and biomass of benthic grazers were quantified from the shoreline down to 3 m depth. Samples were collected by a diver at 0.1, 1, 2, and 3 m depth using 20 × 20 cm frames placed randomly on the sea floor. Three replicates were taken at each depth. All mussels within the frame were collected and their length was measured to the nearest 0.1 mm using a Vernier caliper. Animals were dried with shells at 60 °C for 48 h and their dry weight (DW) determined.

Mesozooplankton was sampled by a 90-μm net from the upper 1 m of the water column. Samples were preserved in 4% formaldehyde solution and counted subsequently under binocular microscope following the standardized procedure of HELCOM (http://www.helcom.fi/groups/monas/CombineManual/PartC/en_GB/main/#c4, HELCOM 1988). Biomasses (wet weights) were calculated using the biomass factors for different taxonomic groups and developmental stages (Hernroth 1985). Microzooplankton samples were taken from the surface water and preserved in acid Lugol solution. Samples were concentrated before counting in 50-ml tube, animals were counted under an inverted microscope and their wet weights (WW) were calculated by formulas based on the volume of animals.

Community grazing rates were expressed as the average amount of Chl *a* removed from the water column above 1-m^2 bottom area in the depth range of 0.1–3 m. This range was chosen as the density of BSF quickly decreases at greater depths in the studied sites. The biodeposition rates of BSF were multiplied by the average biomasses at a site in the same season and these values were used as average estimates of benthic grazing in the area. For pelagic grazing, experimental results were extrapolated to the whole water column. Pelagic grazing was assumed to be homogeneous both vertically and horizontally due to an intense wind-induced mixing of the water column.

Grazing rates of benthic and pelagic suspension feeders at the studied sites were compared by factorial ANOVA and ANCOVA. Residual analysis was performed to test the assumptions for parametric tests. Relationships between grazing and environmental variables were tested by factorial ANOVA and linear multiple regression (StatSoft, Inc. 2007). Community data analyses were performed using the statistical program PRIMER version 6.1.5 (Clarke & Gorley 2006). The spatial and temporal

variability of species composition and biomass structure of pelagic suspension feeders was analysed by ANOSIM and contributions of different species to the variability were assessed by SIMPER (Clarke 1993).

Results

Water salinity, temperature, velocity and Chl a content did not differ statistically among the studied sites and seasons (2-way ANOVA, P > 0.05). The Chl a measurements with data logger at the Kõiguste site showed mostly stable Chl a concentrations until the autumn, when we observed a pronounced peak in September (Fig. 3). Phytoplankton communities were generally dominated by diatoms and dinoflagellates (Fig. 4). Benthic suspension feeders had significantly different species composition and biomasses at different sites, whereas seasonal variability was not important (2-way ANOVA, for site $F_{3,41} = 6.52$, P = 0.001, for season P > 0.05). The biomass of BSF was related to salinity, temperature and water Chl a content (multiple regression, R = 0.54, $F_{3,40} = 5.59$, P = 0.003) but not to phytoplankton production (P > 0.05). All sites were characterized by the marine bivalve *Mytilus trossulus* except Audrurand, where the brackish water bivalve *Dreissena polymorpha* prevailed over *M. trossulus*. The biomass of bivalves was about 10 times higher at Audrurand than at the other sites (Table 1). *Mytilus trossulus* had the highest biomasses at 3 m depth except for Kõiguste Bay, where the species had a maximum biomass at 2 m depth. The biomass of *D. polymorpha* had a clear maximum at 3 m depth (Fig. 5). The biomass of *M. trossulus* was positively related to water velocity and salinity and negatively related to water Chl a content (multiple regression, R = 0.63, $F_{3,40} = 8.53$, P < 0.001). The biomass of *D. polymorpha* was positively related to both water temperature and Chl a content (multiple regression, R = 0.55, $F_{2,41} = 8.90$, P < 0.001). Microzooplankton bio-

mass was higher at the sheltered Rame and Kuressaare sites (ANOVA, $F_{3,20} = 36.4$, P < 0.0001), while total mesozooplankton biomass was higher at the Audrurand site (ANOVA, $F_{3,23} = 7.16$, P < 0.001) (Table 1, Fig. 6). The biomass of microzooplankton was negatively related to water salinity (regression analysis, R = 0.54, $F_{1,22} = 9.14$, P = 0.006). The biomass of meroplankton was positively related to water Chl a content (regression analysis, R = 0.75, $F_{4,22} = 7.22$, P < 0.001) and the biomass of other mesozooplankton was positively related to water temperature and salinity (multiple regression, R = 0.81, $F_{4,22} = 10.24$, P < 0.0001). The species composition of microzooplankton was similar at all studied sites but differed significantly between different seasons (ANOSIM, $r_{spring/summer} = 0.89$, P = 0.029, $r_{spring/autumn} = 0.72$,

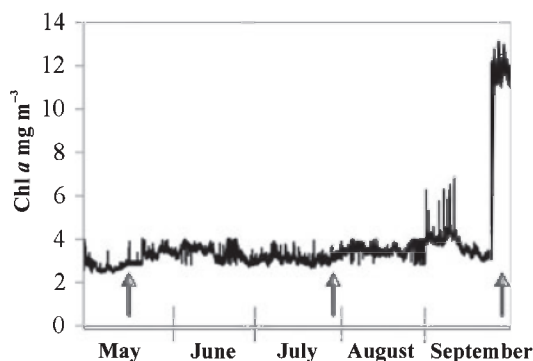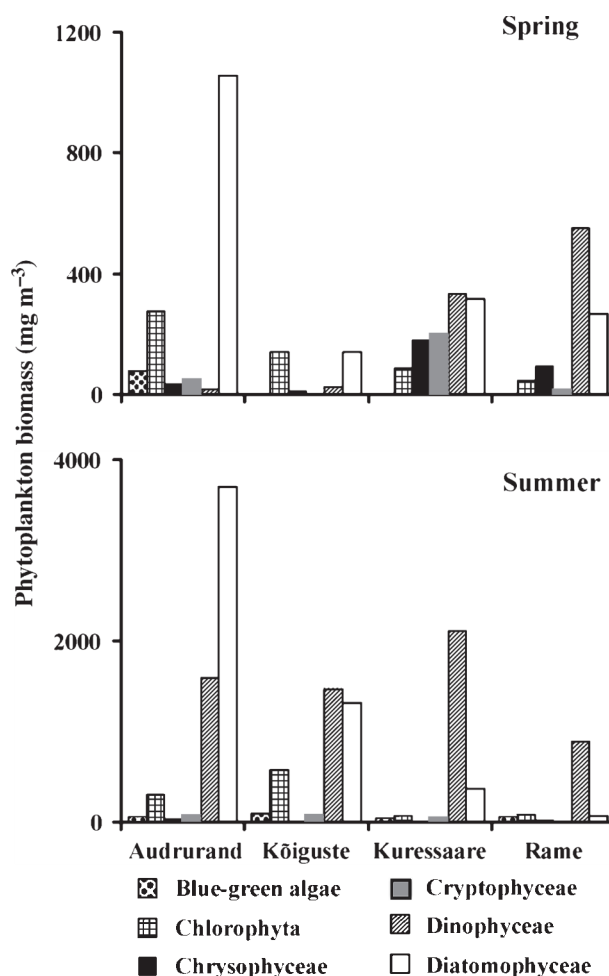**Fig. 4.** Biomasses (wet weights) of phytoplankton taxa at study sites at the time of experiments. Autumn values are excluded due to methodological difficulties in processing (highly turbid samples). Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.

Fig. 3. Logger recordings for water Chl a content at the Kõiguste site in 2003. Arrows indicate the dates of experiments.
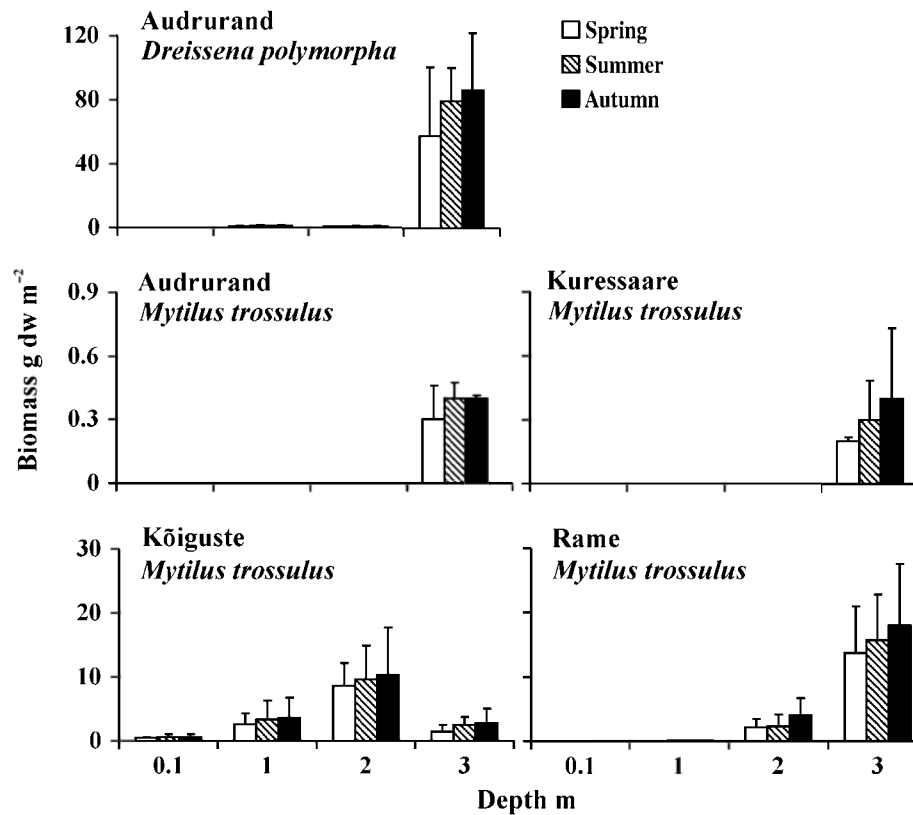
Fig. 5. Biomasses (dry weights with shells) of benthic suspension feeder species at different depths and seasons. Vertical bars indicate SE values. Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.

Fig. 6. Biomasses (wet weights) of meso- and microzooplankton taxa at study sites. Vertical bars indicate SE values. Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.
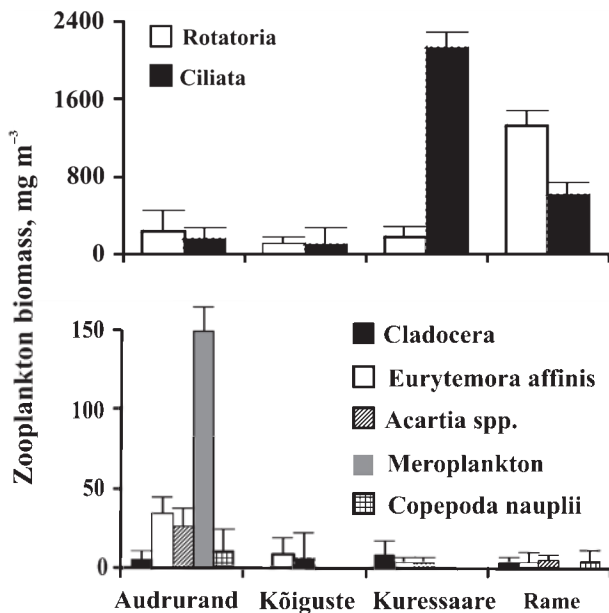
$P = 0.008$ and $r_{summer/autumn} = 0.58$, $P = 0.003$). *Notholca* sp., *Strobilidium* sp. and *Vorticella* sp. were the most typical species in spring, *Keratella quadrata* (Müller), *Strobilidium* sp., *Synchaeta baltica* Ehrenberg and *Keratella cochlearis* (Gosse) in summer and *Strobilidium* sp. and *Strombidium* sp. in autumn (PRIMER, SIMPER, contribution of a single species to the similarity of sample group >10%). The species composition of mesozooplankton was similar among study sites and seasons (PRIMER, ANOSIM, $P > 0.05$).

Pelagic suspension feeders had significantly higher grazing rates than benthic suspension feeders and both site and season affected the grazing rates (ANOVA, Table 2, Fig. 7). Pelagic grazing exceeded benthic grazing 13.7 ± 8.4 times at Audrurand, 39.8 ± 17.3 times at Kõiguste, 56.2 ± 22.7 times at Rame and 4818 ± 1617 times at Kuressaare. Differences in water Chl a content and, to a lesser extent, in phytoplankton production significantly explained the observed effects of site and season (ANCOVA, Table 2).

Benthic suspension feeder *D. polymorpha* had significantly higher grazing rates than *M. trossulus* at Audrurand where two mussel species co-existed (2-way ANOVA with

Table 2. Differences in grazing rates between benthic and pelagic suspension feeders. Grazing rate – the amount of Chl a removed from the water column from 0.1–3 m depth h^{-1}.

	df	F	P
ANOVA			
Site	3	54.19	<0.0001
Season	2	42.52	<0.0001
Suspension feeder group	1	293.26	<0.0001
Site × season	6	42.87	<0.0001
Site × suspension feeder group	3	46.67	<0.0001
Season × suspension feeder group	2	49.68	<0.0001
Site × season × suspension feeder group	6	40.68	<0.0001
ANCOVA			
Temperature			ns
Salinity			ns
Water velocity			ns
Water Chl a	1	36.48	<0.0001
Phytoplankton production	1	9.29	0.003
Suspension feeder group	1	25.84	<0.0001
df error for ANOVA	65		
df error for ANCOVA	73		

season as an additional factor $F_{1,12} = 8.44$, P = 0.01). Different grazing rates resulted from different population sizes of these species at Audrurand. Biodeposition rates for 20-mm individual mussels were similar for both species (ANOVA, P > 0.05).

When suspension feeder groups were analysed separately, it appeared that for benthic suspension feeders, only site modulated the grazing rates (2-way ANOVA, $F_{3,32\ \text{site}} = 12.68$, P < 0.0001). The grazing rate of BSF was not related to any of the measured environmental factors (multiple regression, P > 0.05, Fig. 8); however, there was a high scatter between sites (Fig. 9). For pelagic suspension feeders, site, season and their interactions affected the grazing rates (2-way ANOVA, $F_{3,24\ \text{site}} = 42.76$, $F_{2,24\ \text{season}} = 41.28$ and $F_{6,24\ \text{site x season}} = 35.16$, P < 0.0001). When all sites were pooled together, the grazing rate of pelagic suspension feeders was positively related to water Chl a content but not to phytoplankton production (regression analysis, R = 0.72, $F_{2,33} = 17.15$, P < 0.001, Fig. 8).

Discussion

The results show that benthic suspension feeders removed much smaller amounts of phytoplankton biomass than pelagic suspension feeders did in our study area. Several studies have indicated 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 our study area (Kautsky & Evans 1987; Kotta et al. 2005). 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 bottom boundary layer (Slinn & Riley 1996), reducing near-bottom food limitation for BSF. Indeed, it has been shown that at steeper slopes, there is no food limitation for the benthic communities (Kotta et al. 2007). The steep slopes characteristic of the rocky habitats of the Northern Baltic archipelago areas may therefore account for the capacity of these areas to host noticeably larger biomasses of benthic suspension feeders than those recorded in our study area. BSF-driven energy fluxes also play an important role in large river mouths in various

Fig. 7. Grazing by benthic and pelagic suspension feeders at studied sites and times. Grazing is estimated as the average amount of Chl a removed from the water column above 1-m^2 bottom area in the depth range 0.1–3 m. Vertical bars indicate SE values. Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.
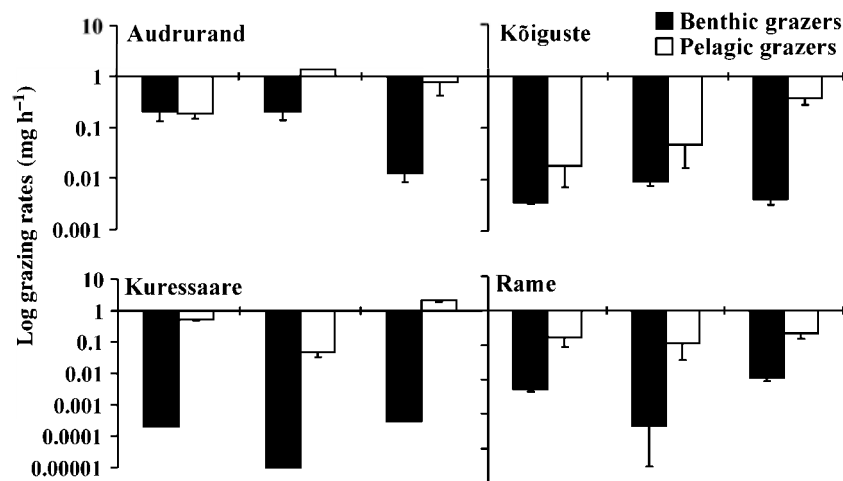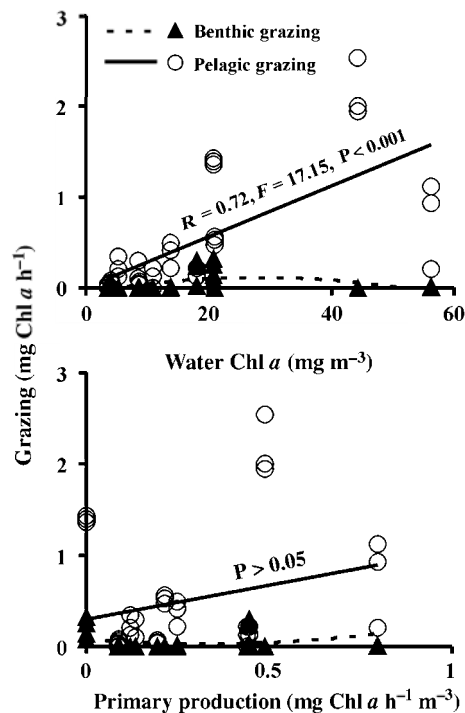
Fig. 8. Benthic and pelagic grazing rates related to water Chl *a* content and phytoplankton primary production in the study area. Grazing is estimated as the average amount of Chl *a* removed from the water column above 1-m² bottom area in the depth range of 0.1–3 m.

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 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, our results indicate that in flat coastal habitats away from large rivers and upwelling areas, benthic suspension feeders play only a minor role in food-web dynamics, and pelagic processes strongly dominate over benthic–pelagic coupling. Such habitats are widespread and typical for the Northeastern Baltic Sea and likewise in coastal areas of South Africa, Arctic, and Antarctic seas, to name just a few (Gutt 2001; Bownes & McQuaid 2006; Kotta *et al.* 2008).

We found that site location was the best predictor of the grazing rates of the BSF, while season and water Chl *a* content were the best predictors for pelagic grazing rates. Site-specific characteristics can influence the balance between pelagic and benthic grazing. Exposure is connected to long-term patterns of water velocity. Benthic grazers are often faced with a limited food supply (Wildish & Kristmanson 1984), which can be extremely harsh at sheltered sites. BSF are also sensitive to oxygen deficiency, which may become crucial in very sheltered sites (Riisgård & Poulsen 1981; Møller & Riisgård 2007). Westerbom & Jattu (2006) hypothesized that higher sedimentation may restrict recruitment of BSF at less exposed
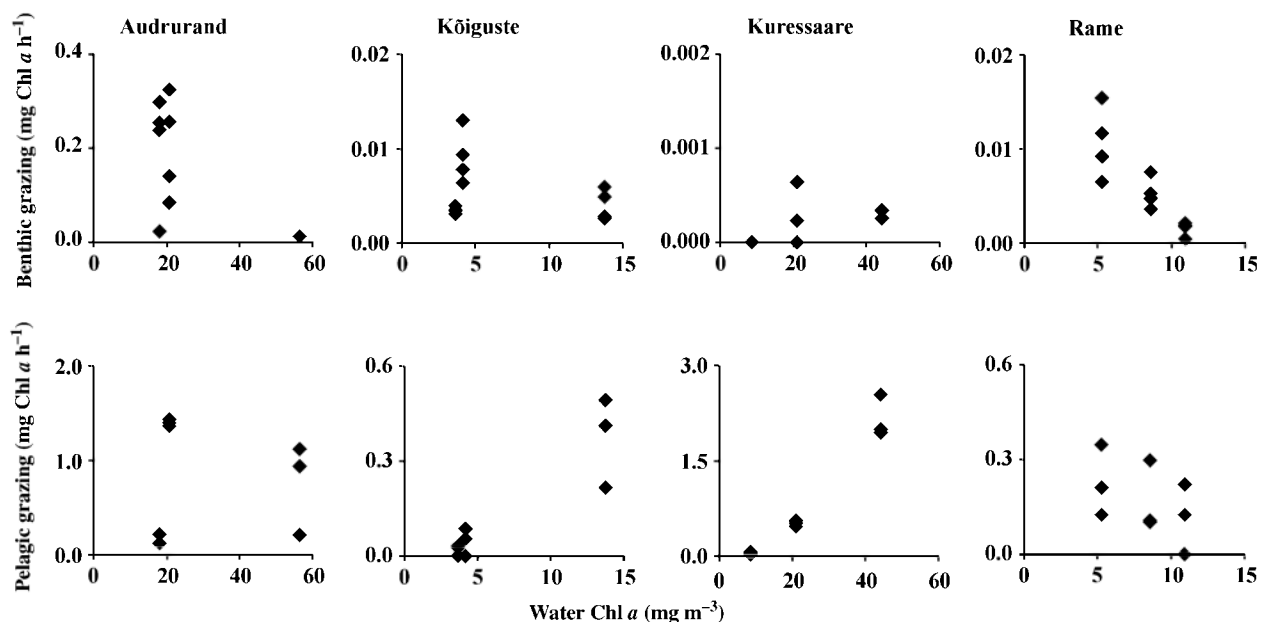

Fig. 9. The site-specific scatter of benthic and pelagic grazing related to water Chl *a* content. Grazing is estimated as the average amount of Chl *a* removed from the water column above 1-m² bottom area in the depth range of 0.1–3 m. Audrurand – eutrophic exposed, Kõiguste – non-eutrophic exposed, Kuressaare – eutrophic sheltered and Rame – non-eutrophic sheltered site.

localities, which is reflected in population sizes. On the other hand, high water velocities at the exposed Audru-rand site suspend lots of clay particles in the water column that may inhibit pelagic grazers (Levine *et al.* 2005). The different relationships between water Chl *a* content and benthic and pelagic grazing likely indicate the ability of pelagic grazers to adjust their grazing rates to the dynamics of phytoplankton. PSF have been shown to increase their abundance quickly in response to high food levels (*e.g.* Martin 1970; Banse 1994). BSF, on the other hand, are not capable of following short-term dynamics of phytoplankton as they can only modulate their feeding activity (Fréchette & Bourget 1987) but cannot effectively multiply or reduce their abundance and biomass in response to phytoplankton fluctuations. Conversely, very high phytoplankton concentrations have been shown to inhibit mussel feeding (Clausen & Riisgård 1996) and may induce oxygen depletion in near-bottom water (Cloern 2001). Our results may hint that complex environmental variables such as eutrophication and exposure which describe systems at longer time scales are appropriate descriptors of benthic grazing, whereas single environmental variables that reflect processes at short time scales can effectively describe the dynamics of pelagic grazing. On the other hand, the biomass and grazing rate of pelagic grazers showed both high temporal and spatial variability in our study. However, as benthic and pelagic grazing are concurrent processes, ecosystem functioning traits such as the prevalence of benthic–pelagic or pelagic–pelagic links in the system may depend on the values of both integrated and single environmental parameters affecting either the benthic or the pelagic component of the system. To estimate benthic grazing rates in coastal sea areas, a low frequency high spatial resolution sampling regime seems to be appropriate, while for pelagic grazing rates both high time and space resolutions may be necessary. To follow the long-term changes in benthic–pelagic coupling the temporal resolution required for the mapping of benthic grazing may be even less than seasonal resolution in our study area. Data from *in situ* loggers (see Material and Methods section) indicated a stochastic, presumably wind-induced weekly or monthly variance in water Chl *a* content. Pelagic grazing was strongly related to water Chl *a* content in the present study, therefore the observations on pelagic grazing should match the scale of variability in Chl *a* concentration, *i.e.* they should be performed on weekly basis.

Usually, studies drawing system-wide conclusions have been focused on either benthic or pelagic suspension feeders, and the role of one group is investigated separately, paying no special attention to the potential role of the other group. Among the few exceptions are the Great Lakes where the recent invasions of *D. polymorpha* and

Dreissena bugensis resulted in questions about the potential re-arrangement of pelagic food webs due to an addition of an almost completely new function to the ecosystem. This stimulated a small cascade of studies addressing the potential food competition between zooplankton and dreissenids in some lakes (Bridgeman *et al.* 1995; Horgan & Mills 1999; Noonburg *et al.* 2003; Conroy *et al.* 2005). However, the conclusions from these studies have been controversial for different and even the same localities (Wu & Culver 1991; MacIsaac *et al.* 1992) and the actual role of Dreissenids in ecosystem functioning remains under debate.

While the above-mentioned studies concentrated on ecosystems in non-equilibrium state, the problem remains similarly unresolved for more mature communities. For example, BSF, light limitation, tidal mixing, and low residence time are all considered possible causes of low phytoplankton biomass in San Francisco Bay (Cloern 2001). In the majority of food-web studies, food consumption pathways are addressed rather than competitive or more complicated interactions (Paine 1994). Indeed, BSF are able to consume their pelagic competitors in addition to other seston (MacIsaac *et al.* 1991; Wong *et al.* 2003; Prins & Escaravage 2005), but the scope of other interactions between these feeding modes seems equally relevant in ecosystem functioning. The majority of research focusing on benthic–pelagic coupling tends to deal with a simplification considering solely the benthic component and its pelagic prey extracted from the real system consisting of a much more complex web of interactions. We might consider that benthic and pelagic suspension feeders are actually consuming the same stock of food at the same time and phytoplankton of shallow water bodies has to deal simultaneously with both benthic and pelagic grazing pressures.

The variability in ecosystem functioning pathways is highly dependent on the energy flow characteristics of the system. Møller & Riisgård (2007) found that BSF were indirectly influenced by predation on pelagic grazers in an eutrophied Danish fjord as algal blooms induced oxygen deficiency in near-bottom water that severely depressed BSF. A study on another trophic cascade reveals traits in the opposite direction in San Francisco Bay, which has been characterized by substantial BSF-mediated energy flows and where increased predation on benthic grazers caused enhanced phytoplankton blooms (Cloern *et al.* 2007). Our results indicate a bigger share of energy flows through PSF, and therefore trophic interactions generating stronger effects may likely operate through pelagic food-webs in our study area.

As BSF recycle nutrients from phytoplankton and facilitate benthic vegetation (Reusch *et al.* 1994; Kotta *et al.* 2006), they are assumed to drive an ecosystem from the

dominance of pelagic to benthic primary production. In such cases, a sustained population of mussels countervailing an abundant phytoplankton stock seems to be an unstable state of an ecosystem. Indeed, a few monitored episodes of an introduction of benthic grazers have shown to result in dramatic and abrupt shifts of ecosystems to a new "steady" state. There is some recent evidence for such unbalancing effects of benthic suspension feeders from a Danish estuary (Petersen *et al.* 2008), San Francisco Bay (Alpine & Cloern 1992) and the Great Lakes (Roberts 1990). Nevertheless, most such examples represent quite "new" equilibria, which seem to be stable in given conditions and chosen time scale but may well prove to be highly dynamic at longer time scales. Our study area represents a typical coastal area of the Northeastern Baltic Sea with low water velocities compared to tidal seas, diffuse nutrient load, lack of upwelling, or nutrient loads from point sources. No shifts in the distribution of BSF have recently taken place (Kotta *et al.* 2008) and the area can probably be characterized as an ecosystem in a stable state (Scheffer *et al.* 2001). *Dreissena polymorpha*, although an invasive species, has already a history of invasion for at least 150 years in the study area (see references in Lauringson *et al.* 2007). In our study area the populations of BSF were dense enough to periodically consume phytoplankton equal to PSF only at an eutrophic exposed site with high water velocities constantly supplying near-bottom layers with food-rich water. It must be noted, however, that the distribution of BSF was spatially limited and BSF showed low feeding rates at high Chl *a* concentrations. Therefore BSF were unlikely to influence phytoplankton dynamics in a system-wide scale or cause any shifts in ecosystem functioning.

The issue of benthic control over pelagic system in estuarine and freshwater habitats has been discussed quite often in recent decades and the probability of such a control has usually been assumed to be high (Cloern 1982; Officer *et al.* 1982; Reeders & Bij de Vaate 1990; Alpine & Cloern 1992; Prins & Escaravage 2005). Although our study is not focussed on the control issues but rather discusses the flows of energy in the coastal ecosystem, the results still suggest factors that may be important in controlling phytoplankton abundance. Phytoplankton is a temporally highly variable food source and therefore challenges its consumers to overcome big fluctuations in food supply. Pelagic suspension feeders have evolved a good strategy to gain maximum profit from that food source, both temporally by mimicking the ephemeral life strategy of their prey and spatially by inhabiting the same habitat. Benthic suspension feeders, on the other hand, are faced with certain difficulties in both spatial and temporal terms. Removing large quantities of phytoplankton would demand (i) access to the whole water column and (ii) surviving the clear-water phases between

phytoplankton blooms with high biomasses to benefit from the blooming phase of phytoplankton. There are clear Chl *a* gradients measured above mussel beds, indicating possible food limitation due to Chl *a* depletion in the near-bottom water layer (Fréchette *et al.* 1989; Dolmer 2000; Ackerman *et al.* 2001) as the water column is not stirred up evenly. Therefore mussels commonly experience suboptimal food conditions in the field and cannot use their maximum filtration potential to remove phytoplankton from the whole water column. Unfortunately, the majority of studies on the grazing potential of benthic suspension feeders have been performed in the laboratory. As the actual grazing potential in the field depends on the availability and refiltration rates of food-rich water, extrapolation from laboratory studies can easily lead to an overestimation of the real consumption. Bigger size also gives BSF an advantage over PSF as it enables BSF to survive clear-water phases and start feeding immediately at the beginning of the bloom. However, the threshold of starvation may depend on the species characteristics, the condition of individuals before the clear-water phase, and the ability of individuals to use additional food sources besides phytoplankton. Several authors have shown that benthic suspension feeders can utilize benthic food sources suspended by waves or tidal currents (Machas *et al.* 2003; Garton *et al.* 2005; Sara 2006). There is a possible scenario for BSF population to use benthic microalgae and detritus during clear-water phases and therefore to be able to maintain sufficient biomass necessary to profit from peak phytoplankton productions. However, in cases of excess food supply, benthic suspension feeders have been shown to reduce their filtration rates (Clausen & Riisgård 1996) and there is a rising evidence that mussels are unable to fully utilize phytoplankton blooms (Kotta & Møhlenberg 2002; Caraco *et al.* 2006). In our study, mussels reached the highest biomasses in an exposed eutrophic area, indicating that food supply was the limiting factor for mussel distribution. However, grazing by the mussel population did not increase with Chl *a* levels as did pelagic grazing, and was low at high Chl *a* values. We suggest that the periods of low phytoplankton availability limited the grazing potential of the mussel population even at the exposed eutrophic area. It is reasonable to argue that the density of mussel populations at our study sites reflects the optima to survive clear-water phases rather than to utilize fully the peak phases of phytoplankton.

Conclusions

The populations of BSF grazed considerably less phytoplankton than the populations of PSF in the flat coastal habitats of the Northeastern Baltic Sea. 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 showed both spatial and temporal variability and were related to water Chl *a* content. Our results may indicate that in stable-state non-tidal coastal habitats with no steep bottom slopes or direct riverine inputs, BSF-driven energy flows play only a minor role in food-web dynamics compared to pelagic processes.

Acknowledgements

References

Ackerman J.D., Loewen M.R., Hamblin P.F. (2001) Benthic-pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnology and Oceanography*, **46**, 892–904.

Alpine A.E., Cloern J.E. (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography*, **37**, 946–955.

Banse K. (1994) Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. *Oceanography*, **7**, 13–20.

Bownes S.J., McQuaid C.D. (2006) Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa? *Journal of Experimental Marine Biology and Ecology*, **338**, 140–151.

Bridgeman T.B., Fahnenstiel G.L., Lang G.A., Nalepa T.F. (1995) Zooplankton grazing during the zebra mussel (*Dreissena polymorpha*) colonization of Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, **21**, 567–573.

Bushek D., Allen D.M. (2005) Motile suspension feeders in estuarine and marine ecosystems. In: Dame R.F., Olenin S. (Eds), *The Comparative Roles of Suspension-Feeders in Ecosystems*. Springer, Dordrecht: 53–71.

Caraco N.F., Cole J.J., Strayer D.L. (2006) Top-down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. *Limnology and Oceanography*, **51**, 664–670.

Clarke K.R. (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Clarke K.R., Gorley R.N. (2006) *Primer v6. User Manual/Tutorial*. Primer-E, Plymouth, UK: 192 pp.

Clausen I., Riisgård H.U. (1996) Growth, filtration and respiration in the mussel *Mytilus edulis*: no evidence for physiological regulation of the filter-pump to nutritional needs. *Marine Ecology Progress Series*, **141**, 37–45.

Cloern J.E. (1982) Does the benthos control phytoplankton biomass in South San Francisco Bay? *Marine Ecology Progress Series*, **9**, 191–202.

Cloern J.E. (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, **210**, 223–253.

Cloern J.E., Jassby A.D., Thompson J.K., Hieb K.A. (2007) A cold phase of the East Pacific triggers new phytoplankton blooms in San Francisco Bay. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18561–18565.

Conroy J.D., Edwards W.J., Pontius R.A., Kane D.D., Zhang H., Shea J.F., Richey J.N., Culver D.A. (2005) Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. *Freshwater Biology*, **50**, 1146–1162.

Daunys D., Zemlys P., Olenin S., Zaiko A., Ferrarin C. (2006) Impact of the zebra mussel *Dreissena polymorpha* invasion on the budget of suspended material in a shallow lagoon ecosystem. *Helgoland Marine Research*, **60**, 113–120.

Dolmer P. (2000) Algal concentration profiles above mussel beds. *Journal of Sea Research*, **43**, 113–119.

Fréchette M., Bourget E. (1987) Significance of small-scale spatio-temporal heterogeneity in phytoplankton abundance for energy flow in *Mytilus edulis*. *Marine Biology*, **94**, 231–240.

Fréchette M., Butman C.A., Geyer W.R. (1989) The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnology and Oceanography*, **34**, 19–36.

Garton D.W., Payne C.D., Montoya J.P. (2005) Flexible diet and trophic position of dreissenid mussels as inferred from stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 1119–1129.

Gutt J. (2001) On the direct impact of ice on marine benthic communities, a review. *Polar Biology*, **24**, 553–564.

HELCOM (1988) Guidelines for the Baltic Monitoring Programme for the third stage. Part D. Biological determinants. *Baltic Sea Environment Proceedings*, **27D**, 161.

Hernroth L. (1985) Recommendations on methods for marine biological studies in the Baltic Sea. Mesozooplankton assessment. *BMB Publication*, **10**, 1–32.

Horgan M.J., Mills E.L. (1999) Zebra mussel filter feeding and food-limited production of *Daphnia*: recent changes in lower trophic level dynamics of Oneida Lake, New York, U.S.A. *Hydrobiologia*, **411**, 79–88.

Jackson G.A. (1980) Phytoplankton growth and zooplankton grazing in oligotrophic oceans. *Nature*, **284**, 439–441.

Kautsky U. (1995) Ecosystem processes in coastal areas of the Baltic Sea. PhD dissertation, Stockholm University.

Kautsky N., Evans S. (1987) Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Marine Ecology Progress Series*, **38**, 201–212.

Kiørboe T., Møhlenberg F. (1981) Particle selection in suspension feeding bivalves. *Marine Ecology Progress Series*, **5**, 291–296.

Kotta J., Møhlenberg F. (2002) Grazing impact of *Mytilus edulis* and *Dreissena polymorpha* (Pallas) in the Gulf of Riga,

Baltic Sea estimated from biodeposition rates of algal pigments. *Annales Zoologici Fennici*, **39**, 151–160.

Kotta J., Orav-Kotta H., Vuorinen I. (2005) Field measurements on the variability in biodeposition and estimates of grazing pressure of suspension feeding bivalves in the northern Baltic Sea. In: Dame R.F., Olenin S. (Eds), *The Comparative Roles of Suspension-Feeders in Ecosystems.* Springer, Dordrecht: 11–29.

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.

Kotta J., Lauringson V., Kotta I. (2007) Response of zoobenthic communities to changing eutrophication in the northern Baltic Sea. *Hydrobiologia*, **580**, 97–108.

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.* Springer, Berlin: 217–243.

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 freshwater populations. *Estuarine, Coastal and Shelf Science*, **75**, 459–467.

Levine S.N., Zehrer R.F., Burns C.W. (2005) Impact of resuspended sediment on zooplankton feeding in Lake Waihola, New Zealand. *Freshwater Biology*, **50**, 1515–1536.

Lundberg J., Moberg F. (2003) Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, **6**, 87–98.

Machas R., Santos R., Peterson B. (2003) Tracing the flow of organic matter from primary producers to filter feeders in Ria Formosa lagoon, southern Portugal. *Estuaries*, **26**, 846–856.

MacIsaac H.J., Sprules W.G., Leach J.H. (1991) Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics? *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2051–2060.

MacIsaac H.J., Sprules W.G., Johannsson O.E., Leach J.H. (1992) Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia*, **92**, 30–39.

Martin J.H. (1970) Phytoplankton-zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. *Limnology and Oceanography*, **15**, 413–418.

Møller L.F., Riisgård H.U. (2007) Impact of jellyfish and mussels on algal blooms caused by seasonal oxygen depletion and nutrient release from the sediment in a Danish fjord. *Journal of Experimental Marine Biology and Ecology*, **351**, 92–105.

Noonburg E.G., Shuter B.J., Abrams P.A. (2003) Indirect effects of zebra mussels (*Dreissena polymorpha*) on the planktonic food web. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1353–1368.

Norkko A., Hewitt J.E., Thrush S.F., Funnell G.A. (2001) Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnology and Oceanography*, **46**, 2067–2072.

Norling P., Kautsky N. (2007) Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. *Marine Ecology Progress Series*, **351**, 163–175.

O'Riordan C.A., Monismith S.G., Koseff J.R. (1995) The effect of bivalve excurrent jet dynamics on mass transfer in a benthic boundary layer. *Limnology and Oceanography*, **40**, 330–344.

Officer C.B., Smayda T.J., Mann R. (1982) Benthic filter feeding: a natural eutrophication control. *Marine Ecology Progress Series*, **9**, 203–210.

Orlova M., Golubkov S., Kalinina L., Ignatieva N. (2004) *Dreissena polymorpha* (Bivalvia: Dreissenidae) in the Neva Estuary (eastern Gulf of Finland, Baltic Sea): is it a biofilter or source for pollution? *Marine Pollution Bulletin*, **49**, 196–205.

Paine R.T. (1994) *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective. Excellence in Ecology Book 4.* Ecology Institute, Oldendorf/Luhe: 152 pp.

Petersen J.K., Hansen J.W., Laursen M.B., Clausen P., Carstensen J., Conley D.J. (2008) Regime shift in a coastal marine ecosystem. *Ecological Applications*, **18**, 497–510.

Prins T., Escaravage V. (2005) Can bivalve suspension-feeders affect pelagic food web structure? In: Dame R.F., Olenin S. (Eds), *The Comparative Roles of Suspension-Feeders in Ecosystems.* Springer, Dordrecht: 31–51.

Reeders H.H., Bij de Vaate A. (1990) Zebra mussels (*Dreissena polymorpha*): a new perspective for water quality management. *Hydrobiologia*, **200/201**, 437–450.

Reusch T.B.H., Chapman A.R.O., Gröger J.P. (1994) Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Marine Ecology Progress Series*, **108**, 265–282.

Riisgård H.U., Poulsen E. (1981) Growth of *Mytilus edulis* in net bags transferred to different localities in a eutrophicated Danish fjord. *Marine Pollution Bulletin*, **12**, 272–276.

Roberts L. (1990) Zebra mussel invasion threatens U.S. waters. *Science*, **249**, 1370–1372.

Sara G. (2006) Hydrodynamic effects on the origin and quality of organic matter for bivalves: an integrated isotopic, biochemical and transplant study. *Marine Ecology Progress Series*, **328**, 65–73.

Scheffer M., Carpenter S., Foley J.A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Slinn D.N., Riley J.J. (1996) Turbulent mixing in the oceanic boundary layer caused by internal wave reflection from sloping terrain. *Dynamics of Atmospheres and Oceans*, **24**, 51–62.

StatSoft, Inc. (2007) *Electronic Statistics Textbook*. StatSoft, Tulsa, OK. Cited 9 Oct. 2008. Online: http://www.statsoft.com/textbook/stathome.html.

Strickland J.D.H., Parsons T.R. (1972) A practical handbook of seawater analysis. *Bulletin Fisheries Research Board of Canada*, **167**, 1–310.

Viitasalo M., Rosenberg M., Heiskanen A.-S., Koski M. (1999) Sedimentation of copepod fecal material in the coastal northern Baltic Sea: where did all the pellets go? *Limnology and Oceanography*, **44**, 1388–1399.

Westerbom M., Jattu S. (2006) Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. *Marine Ecology Progress Series*, **306**, 191–200.

Wildish D.J., Kristmanson D.D. (1984) Importance to mussels of the benthic boundary layer. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1618–1625.

Wong W.H., Levinton J.S., Twining B.S., Fisher N. (2003) Assimilation of micro- and mesozooplankton by zebra mussels: a demonstration of the food web link between zooplankton and benthic suspension feeders. *Limnology and Oceanography*, **48**, 308–312.

Wu L., Culver D.A. (1991) Zooplankton grazing and phytoplankton abundance: an assessment before and after invasion of *Dreissena polymorpha*. *Journal of Great Lakes Research*, **17**, 425–436.