IMPACT OF EUTROPHICATION AND BIOLOGICAL INVASIONS ON THE STRUCTURE AND FUNCTIONS OF BENTHIC MACROFAUNA

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I. Kotta, J. & Möhlenberg, F. Grazing impact of *Mytilus edulis* L. and *Dreissena polymorpha* (Pallas) in the Gulf of Riga, Baltic Sea estimated from biodeposition rates of algal pigments and biogenic silicate (submitted to *Ophelia*).


III. Kotta, J. & Ólafsson, E. Competition for food between the introduced polychaete *Marenzelleria viridis* and the resident amphipod *Monoporeia affinis* in the Baltic Sea (manuscript).


VII. Kotta, J. & Rissanen, J. Benthic faunal assemblages in the shallow water areas of the Gulf of Riga (manuscript).

ABSTRACT

Benthic macrofauna was studied in the coastal sea of the north-eastern part of the Baltic Sea. Using multivariate statistics the contribution of different environmental factors to the variability in macrozoobenthic assemblages was computed. Phytobenthos may be considered as the key factor for the development of benthic invertebrate assemblages in the less eutrophicated coastal sea whereas sediment type and the load of nutrients affected macrozoobenthos mostly in more eutrophicated regions. The species diversity was lower in more eutrophicated regions. However, significant changes have taken place in the structure of macrozoobenthic assemblages in the whole study area during last decades.

The effect of eutrophication is expressed as an excessive growth of filamentous algae and the development of dense populations of filter-feeding mussels in the coastal areas. As a consequence of a higher coverage of filamentous algae, the stock of Fucus vesiculosus has notably diminished in wide areas. The most prevalent benthic herbivore, the isopod Idotea baltica, has switched to an alternative habitat and diet. I. baltica preferred Furcellaria lumaticalis as a habitat and Pilayella littoralis as a food. The highest densities of I. baltica were observed in shallower areas, where the proportion of the filamentous epiphyte P. littoralis on F. lumbricalis was highest. Removing fast growing epiphytes, isopods protect slow growing F. lumbricalis against a nuisance alga P. littoralis.

The grazing by the filter-feeding bivalve, Mytilus edulis, was the major sink for algae in the northern part of the Gulf of Riga owing to extensive shallow areas and moderate water exchange. M. edulis grazed 1–8% of the standing stock of phytoplankton per day in May and 31–91% in July. The lower grazing pressure in May was due to a high algal biomass and low temperature limiting the filtration rate of M. edulis. These results suggest that benthic control of phytoplankton is more commonplace in the more enclosed areas of the Baltic Sea than previously thought.

Owing to the large potential effect on the whole ecosystem, the Pontocaspian bivalve Dreissena polymorpha and the North-American polychaete Marenzelleria viridis are ranked among the most influential exotics in the north-eastern Baltic Sea. D. polymorpha has established in most of the coastal sea of the Gulf of Riga and in a few localities in the Gulf of Finland. In more eutrophicated regions, where the abundance of the species is higher, D. polymorpha has an important role as a regulating, linking organism between the pelagic and benthic systems.

M. viridis has invaded the Gulf of Riga, the Väinameri and the western and central parts of the Gulf of Riga. Nowadays it is slowly expanding its distribution area towards the eastern parts of the Gulf of Finland. The population of M. viridis has not yet stabilised in the study area. The establishment of the spe-
cies has been more successful in more eutrophicated regions and in more uniform biotopes. Because of competitive interactions for food *M. viridis* has a potential to reduce the growth of a native amphipod, *Monoporeia affinis*, and, hence, prolong amphipod recruitment and reduce its fecundity.
INTRODUCTION

The Baltic Sea is enclosed by land and communicates with the Atlantic by narrow outlets at its south-western end. Owing to its isolation, short developing time, low salinity and temperature only a limited number of species have been able to adapt to the local conditions. The communities are characterised by a peculiar mixture of marine and lacustrine organisms. Specific brackish-water or endemic forms are nearly absent (Segerstråle 1957, Järvekülg 1979, Hällfors et al. 1981). As a consequence of low biological diversity the ecosystem of the Baltic Sea is very vulnerable to any large scale disturbances (Leppäkoski & Bonsdorff 1989, Bonsdorff et al. 1997a).

As the Baltic Sea ecosystem is subjected to extensive anthropogenic impact, eutrophication (e.g. Rosenberg 1985, Bonsdorff et al. 1997a, 1997b) and biological invasions (Jansson 1994, Olenin & Leppäkoski 1999) are considered the key factors of its dynamics. Since the early 1950s eutrophication has become the main threat to the stability of the Baltic flora and fauna. Nutrient levels have significantly risen, leading to increased benthic and pelagic primary production, decreased water transparency and changes in zoobenthos and fish communities (e.g. Rosenberg et al. 1990, Bonsdorff et al. 1997a, 1997b, Kotta et al. 1998a).

The effect of eutrophication is more pronounced in the coastal areas (Schulz et al. 1992) being expressed by the excessive growth of filamentous algae (Rosenberg 1985, Hull 1987, Gray 1992, Kolbe et al. 1995) and the development of dense populations of filter-feeding mussels (Barnes & Hughes 1988, Kautsky et al. 1992, Kautsky U. 1995, VIII). The changes in the structure of benthic macrophyte assemblages should affect the dynamics of herbivore populations. A key question to be answered is whether herbivores are able to switch into alternative diet and, hence, control the outbreak of benthic filamentous algae.

Owing to their large filtration capacity, the populations of filter-feeding mussels are able to filter major parts of the water column each day (Riisgård & Møhlenberg 1979, Kautsky & Evans 1987), and thereby via grazing directly control the standing stock of pelagic primary producers. Consequently, the filter-feeders are considered to play a key role in the stability of coastal ecosystems (Herman & Scholten 1990). In situ studies quantifying broad-scale effects of bivalve populations are scarce and usually they are based on indirect evidence and modelling approaches (e.g. Cloern 1982, Møhlenberg 1995).

Besides eutrophication, biological invasions have resulted in comparably large-scale ecological changes and economic damage worldwide. The examples of invasions in the 1980s and 1990s have shown that successful exotics may render previously stable systems unbalanced and unpredictable (Leppäkoski 1991, Carlton & Geller 1993, Mills et al. 1993, Carlton 1996, Ruiz et al. 1999) and similarly to eutrophication may severely affect biological diversity in the area (Baker & Stebbins 1965, Gollasch & Leppäkoski 1999, Gollasch et al. 1999).
A number of benthic animals presently living in the Baltic have only recently invaded the area, some only in the last decades or years (Gruszka 1999, Olenin & Leppäkoski 1999). Owing to their large potential effect on the whole ecosystem, the Ponto-Caspian bivalve Dreissena polymorpha (Pallas) and the North American polychaete Marenzelleria viridis (Verrill) are ranked among most influential exotics in the Baltic Sea (Jansson 1994, Olenin & Leppäkoski 1999).

The incredible speed of range expansion and the large ecological effects of D. polymorpha have been widely investigated. As fouling organisms they may also cause major economic costs (e.g. Mills et al. 1993, Gollasch & Leppäkoski 1999). The great filtering capacity (Kryger & Riisgård 1988, Horgan & Mills 1997) gives D. polymorpha a potential to affect phytoplankton communities and via phytoplankton control the stock of zooplankton and planktivorous fish communities (Wu & Culver 1991). Unconsumed proportions (pseudofaeces) are deposited on the benthos, supporting also abundant communities of deposit feeders (McKnight et al. 1993). Studies of the effects of D. polymorpha on pelagic communities originate from fresh water biotopes (Stanczykovska et al. 1975, Reeders et al. 1989). As yet no similar investigation from the Baltic Sea exists. Moreover, background data on the spatial distribution of the mussel in the Baltic Sea are scarce and often unreliable. This is mainly due to the difficulties faced in using remote methods such as grabs and dredges on hard bottom biotopes (Järvekülg 1979, Olenin & Leppäkoski 1999).

The detritus feeding polychaete M. viridis was introduced to Europe at the beginning of the 1980s (Atkins et al. 1987). The polychaete has quickly spread to most parts of the North and Baltic seas (Essink & Kleef 1993, Kotta & Kotta 1998). Despite the fact that the species has become a dominant in many parts of the coastal areas (Zettler 1996, Olenin & Leppäkoski 1999), there are no studies to date that have addressed what effects this polychaete may have on the benthic assemblages. There exists only circumstantial evidence that, after the invasion of M. viridis, the densities of the shallow water amphipod Corophium volutator (Pallas) (Atkins et al. 1987, Zettler 1996), the polychaete Nereis diversicolor (O. F. Müller) (Atkins et al. 1987, Essink & Kleef 1993) and the deep-water amphipod Monoporeia affinis Lindström (Kube et al. 1997) have dropped considerably. On the other hand, M. viridis has become an important food item for some benthophagous fishes in shallow water estuaries (Winkler & Debus 1997).

The aim of this thesis was to estimate the effect of eutrophication and biological invasions on the benthic invertebrates inhabiting the north-eastern Baltic Sea. The main objectives were:

- to estimate the role of eutrophication and human-mediated introductions in the structure and development of benthic invertebrate assemblages
- to investigate the relationships between eutrophication induced changes in the macroalgal community composition and life history of the dominant herbivore species Idotea baltica (Pallas)
• to evaluate the grazing impact of the dominant filter-feeders, *Mytilus edulis* L. and *D. polymorpha*, on the phytoplankton community
• to test whether the introduced polychaete *M. viridis* has a potential to out-compete the native amphipod *M. affinis*.
STUDY AREA

The field investigations were carried out along Estonian and Latvian coasts of the Baltic Sea, from Narva Bay to the Kolka Peninsula (Fig. 1). The areas embrace the Gulf of Finland, the Väinameri Sea, the Gulf of Riga and partly the Baltic Proper.

Figure 1. Sampling stations. Dashed circles indicate sampling areas: I, Kunda Bay (15 stations); II, Tallinn and Muuga bays (40 stations); III, coastal sea off Vormsi Island (15 stations); IV, Väinameri Archipelago (90 stations). Stars represent the stations of the Estonian Coastal Monitoring Programme, solid lines show the location of the transects in the Gulf of Riga.
The major part of this area has salinity around 6 psu. Salinities down to 2 psu were recorded in the easternmost part of the Gulf of Finland and the sea areas adjacent to the Pärnu and Daugava rivers. The salinity of the study area is relatively stable in comparison with conditions which are usually found in estuaries along open oceanic coasts. A strong continental influence upon the hydrography of the shallower parts of the study area is reflected in striking temperature fluctuations, from subtropical conditions in summer to subpolar conditions in winter. Mean temperatures range between −0.4 and 25°C. The coastal types vary from sands to rocks (Segerstråle 1957, Mardiste 1970, Järvekülg 1979, Kullenberg 1981, Winterhalter et al. 1981).

Salinity and temperature conditions together with the unstable geological history of the Baltic have shaped the native flora and fauna. Due to the young age and isolation of the Baltic only a limited number of species have been able to adapt to the local conditions. There is not only the typical mixture of marine, lacustrine and genuine brackish water forms, normally characterising diluted areas, but also Arctic relicts that invaded during the Glacial Ice Age can be found (Segerstråle 1957, Järvekülg 1979, Hällfors et al. 1981).

Nutrient concentrations in the water and, as a consequence, the organic content of the sediments have increased significantly in the study area during the 20th century through increased sedimentation (Jonsson & Carman 1994, Wulff et al. 1994, Leppäkoski & Miheea 1996). Among the most affected areas are the southern and the north-eastern part of the Gulf of Riga (HELCOM 1997) and Tallinn Bay in the middle of the Gulf of Finland (Turro & Jakobson 1997).
MATERIAL AND METHODS

Distribution. At the depths less than 20 m the material for the mapping studies was collected by a SCUBA diver using a Tvärminne (Kangas 1972) or suction sampler (Hiscock & Hoare 1973). Deeper down a van Veen bottom grab was used. Sediment samples were washed through a 0.25 mm mesh. In the laboratory animals were counted under a stereo dissecting microscope. The total dry weight of the animals in each sample was weighed to the nearest 0.5 mg and calculated for an area of 1 m². Multivariate data analyses were performed using the statistical program PRIMER (Clarke & Warwick 1994) (IV–VIII).

Experimental. Grazing rates of *M. edulis* and *D. polymorpha* were estimated on two transects in the southern and northern parts of the Gulf of Riga during May and July 1996. Chlorophyll and biogenic silica in faecal material were used as tracers for planktonic algae (I). Benthic macroalgal production and herbivore grazing were studied at 0.5 m depth in Kõiguste Bay, the Gulf of Riga in July and October 1998. Photosynthetic and respiratory performances of algae were determined by measuring changes in dissolved oxygen concentration in “light” and “dark” bottles. Grazing performance of *I. baltica* on *Pilayella littoralis* Kjellm. and *Furcellaria lumbricalis* J. V. Lamour was calculated from the changes in the wet weight of the algae in the incubation trays (II). Interspecific competition for food between the introduced polychaete *M. viridis* and the native amphipod *Monoporeia affinis* was studied in a laboratory experiment. Amphipods and polychaetes were kept in microcosms with sediment and continuous supply of cooled water for 2 months. At the end of the experiment animals were counted and the length and dry weight of *M. affinis* were measured (III).
RESULTS AND DISCUSSION

Factors affecting the composition, abundance and biomass structure of benthic invertebrate assemblages

Less eutrophicated regions of the north-eastern Baltic Sea (i.e. areas not affected by point source nutrient discharge) had relatively diverse macrozoobenthic assemblages. The factors that described the abundance and biomass structure of benthic invertebrate assemblages varied between different waterbodies. Mainly the type of substrate and vegetation determined the species composition, abundance and biomass of macrozoobenthos in the Gulf of Riga. (1) Crustaceans, oligochaetes and polychaetes were most abundant and burrowing bivalves had highest biomasses in unvegetated soft bottom areas. Highest densities were observed in less eutrophicated areas and lowest in more eutrophicated areas. (2) Vascular plant communities were numerically dominated by insect larvae and gastropods of freshwater origin while the biomass was dominated by burrowing mussels. (3) Mainly phytophilous crustaceans and filter-feeding bivalves were found in the algal communities on hard substrate (VII).

Along with the type of substrate and the vegetation, salinity was the third important variable in explaining the structure of benthic invertebrate assemblages in the Gulf of Riga. Higher proportions of brackish and fresh water species were found in the north-eastern and southern parts of the Gulf, in areas subjected to larger fresh water inflow (VII).

There existed no key environmental variable determining the structure of macrozoobenthos assemblages in the Väinameri Sea. Depth, type of substrate, dominating phytobenthic species and coverage of *F. lumbricalis* gave the best match with the distribution of macrozoobenthos. In the deeper areas (4–10 m) sediment type and the coverage of *F. lumbricalis* had highest impact on macrozoobenthos whereas in the shallower areas (< 4 m) the dominating phytobenthic species were most important (VI).

It was suggested that due to the intensive currents and stochastic storm events the sediments are highly mobile in the shallower parts of the study area (Mardiste 1970, Suursaar et al. 1998). In that respect, macrophytes might offer benthic invertebrates a refuge from sediment mobility and, hence, control the standing stock and diversity of the macrozoobenthos (e.g. Reusch & Chapman 1995). In the deeper areas where the sediments are more stable, the structure of macrozoobenthos is mainly determined by the properties of the substrate, which is primary substrate or an algal canopy. In the deeper parts of the Väinameri (5–9 m) the loose-lying macroalgae *F. lumbricalis* contribute to the increase in the biomass of macrozoobenthos by offering an appropriate substrate for true hard bottom invertebrates, for example *M. edulis*. On the other hand, the
infauna below this algal mat had lower biomasses as compared to the sediments in unvegetated areas. One possible explanation could be the development of temporary hypoxic conditions under the algal mat due to the decomposition of epiphytic filamentous algae attached to *F. lumbricalis* (Norkko & Bonsdorff 1996a, 1996b, VI).

In the relatively clean coastal areas the total abundance and the biomass of macrozoobenthos have not changed significantly during the last decades. There is an indication, however, that due to the mass occurrence of filamentous algae the abundance and the biomass of epibenthic macrofauna have increased in macrovegetation (II, IV). On the other hand, the species diversity has markedly declined in unvegetated areas (VIII). Several species, for example *Idotea chelipes* (Slabber), *Asellus aquaticus* (L.), *Jaera albifrons* coll. Leach. and *Lymnaea peregra* (O. F. Müller), which were common in the 1970s, have become rare in extensive areas. All these species are considered to be phytophilous. Hence, it is likely that the decline in the species diversity reflects the overall impoverishment of the benthic vegetation in the area (VIII).

**More eutrophicated regions**, for example Pärnu Bay and the sea areas adjacent to Riga, had significantly lower benthic diversity than the areas described above. The abundance and biomass structure of macrozoobenthos were mainly determined by the nutrient load, type of substrate and salinity. Filter-feeding bivalves dominated on the hard bottoms, *D. polymorpha* at salinities less than 5 psu and *M. edulis* in the more saline environments. Occasionally these two species were found together in the same samples. Soft bottom assemblages were characterised by the deposit feeding bivalve *Macoma balthica* L. and partly by the deposit-feeding amphipod *C. volutator* (Kotta & Kotta 1995, IV, VII, VIII).

On soft bottoms the diffuse and the point source nutrient supply had a similar effect on the macrozoobenthic species composition and their dominance structure. However, the functional diversity was higher in the areas subjected to diffuse nutrient input in comparison to the areas receiving a point source nutrient discharge (IV).

In the eutrophicated areas the biomass of macrozoobenthos has notably increased during the last decades. Similarly to the cleaner coastal sea, many phytophilous species have considerably reduced their distribution area. The most uniform assemblages have developed in the localities where the highest load of nutrients was recorded (Kotta & Kotta 1995, VIII).

To conclude, the phytobenthos may be considered a factor of prime importance for the development of benthic invertebrate assemblages in the cleaner coastal sea whereas the sediment and load of nutrients affected macrozoobenthos mostly in more eutrophicated regions. The species diversity was significantly lower in more eutrophicated regions (e.g. Pärnu Bay and the estuary of the Daugava River). Notable changes in the structure of macrozoobenthic assemblages have taken place both in less and more eutrophicated regions during the last decades. This is expressed by a reduction of species diversity and an increase in the dominance of filter-feeding bivalves.
Invasion and distribution pattern of *Dreissena polymorpha* and *Marenzelleria viridis*

The Baltic Sea may be regarded as an area that is extraordinarily invasion prone owing to its short geological history, low number of species and intensive freight transportation. Therefore, it is not surprising that several non-indigenous species have been discovered in the Baltic Sea during last decades (Jansson 1994, Gollasch & Leppäkoski 1999, http://www.ku.lt/nemo/mainnemo.htm). Among benthic invertebrates *M. viridis*, *Hemimysis anomala* G. O. Sars and *Orchestia cavimana* Heler are the most recent newcomers in the north-eastern Baltic Sea (Salemaa & Hietalahti 1993, Lagzdins & Pallo 1994, Kotta 2000). Considering the possible impact on the native assemblages, *D. polymorpha* and *M. viridis* are considered to be the most important exotics in the study area.

*Dreissena polymorpha*, a brackish water species of Ponto-Caspian origin, widely expanded its distribution area in Europe owing to the augmented freight transportation by rivers in the beginning of the 19th century (Morton 1969, Rosenberg & Ludyanskiy 1994). The bivalve was first recorded in the Baltic Sea in 1824 (Thienemann 1950) and in Estonian coastal sea in the middle of the 19th century (Schrenk 1848).

Nowadays, the species has been established in a few localities of the easternmost Gulf of Finland (Valovirta & Porkka 1996, Kotta *et al.* 1998b) and in less saline parts of the Gulf of Riga (Kotta *et al.* 1998b, VII). *D. polymorpha* has not been found in the Väinameri.

New findings of *D. polymorpha* in the coastal area of the Gulf of Finland indicate that a slow expansion of its distribution area is currently taking place. However, the Gulf of Finland is a relatively hostile environment for *D. polymorpha*, which originates from the warmer areas. The population seems to be unstable and the species is likely to reproduce only occasionally in favourable years (Valovirta & Porkka 1996, Kotta *et al.* 1998b).

*D. polymorpha* is relatively common everywhere in the Gulf of Riga except in its middle part and at the southern coast of Saaremaa Island (Kotta *et al.* 1998b). The distribution area documented in the literature (Shurin 1953, 1961, Järvekülg 1979) is fairly consistent with my findings with the exception that Shurin (1961) also found a population of *D. polymorpha* living on phanerogams in the southern coastal sea off Saaremaa Island.

*D. polymorpha* inhabits depths down to 15 m when suitable substrate, *i.e.* hard bottoms or macrovegetation with strong thalli, is present. The biomass of *D. polymorpha* was significantly higher on stone bottoms followed by vegetated and mixed bottoms. Sediment type did not contribute to the variance of the abundance of *D. polymorpha* (Kotta *et al.* 1998b).

Generally, the abundances and biomasses of the species were low, around 50 ind m\(^{-2}\) and 5 g dw m\(^{-2}\), respectively. The values up to 8400 ind m\(^{-2}\) and 1400 g dw m\(^{-2}\) were recorded in the southernmost part of the Gulf of Riga. This
could be explained by the inflow of fresh water of the Daugava River resulting in lower salinity and higher nutrient concentrations and, consequently, higher phytoplankton biomass (Kotta et al. 1998b, I).

Hence, the factors favouring the development of a dense population of *D. polymorpha* are rather low salinity (< 5 psu) and high trophic conditions (chl *a* values during spring bloom > 20 µg l⁻¹). In the areas of higher salinity (> 5 psu) lower filtration rates set the limits of its distribution and the species is probably outcompeted by *M. edulis* (I).

The North American polychaete *Marenzelleria viridis* was for the first time found in European waters, in Scotland, in 1982 (Atkins et al. 1987). It is assumed that the species was introduced into Europe with ballast water. In 1985 *M. viridis* was reported from the Baltic Sea (Bick & Buckhardt 1989) and since then the species has established practically along all coasts of the Baltic Proper, the Gulf of Finland and the Gulf of Riga (Essink & Kleef 1993, Kotta & Kotta 1998, V).

*M. viridis* was observed for the first time in the Gulf of Riga, near the mouth of the Daugava in 1988 (Lagzdins & Pallo 1994). The following four years the polychaete densities rose more than 100 times reaching the values of 1400 ind m⁻². In the northern part of the Gulf of Riga and the Väinameri *M. viridis* was found in 1995. The salinity values were relatively stable at the beginning of the 1990s whereas average temperatures were much higher in 1994 than in previous years. Probably, higher summer temperature resulted in a higher reproductive output of *M. viridis*, which enhanced its invasion ability towards the northern part of the Gulf of Riga and the Väinameri (Kotta & Kotta 1998). According to invasion meltdown hypothesis (Simberloff & Von Holle 1999) cumulative invasions facilitate one another’s establishment and continued existence instead of interfering with one another. Thus, the appearance of *M. viridis* at the northern coasts of the Gulf of Riga and the Väinameri might be a consequence of previous unsuccessful invasions.

The first observation of *M. viridis* at the northern coast of the Gulf of Finland was made in 1990 (Norkko et al. 1993, Stigzelius et al. 1997). During 1990–1993 *M. viridis* expanded its distribution into the eastern parts of the Gulf (Stigzelius et al. 1997). However, anti-clockwise circulation of the currents would not permit *M. viridis* to spread from the northern side of the Gulf of Finland towards its southern side. In addition, the larvae of the polychaete are unable to complete their development at salinities below 5 psu (George 1966), which may frequently occur in the easternmost part of the Gulf of Finland. Only one specimen was recorded near the Pühajõgi River, south-eastern coast of the Gulf of Finland, in 1994. Until 1997 this polychaete was not observed along the southern coast of the Gulf of Finland. Some occasional findings of *M. viridis* in the westernmost bays of the Gulf of Finland suggest the Väinameri as a donor region. Nowadays *M. viridis* is slowly expanding its distribution range towards the eastern parts of the Gulf of Finland, being established as far as in Tallinn Bay (Kotta & Kotta 1998).
Depth did not correlate with the abundance and biomass of *M. viridis* but sediment type was a significant factor for both. In shallower areas (< 10 m) *M. viridis* preferred sand or gravel bottoms. Its abundance was higher in more densely vegetated areas. Deeper down (> 10 m) *M. viridis* was confined to silty clay bottoms (Kotta & Kotta 1998).

In the Väinameri the polychaete was restricted to deeper parts of the archipelago (7–11 m). The area is homogeneous both in terms of sediment and macrovegetation: the sandy clay substrate is covered with a loose layer of the red algae *F. lumbricalis*. Among benthic invertebrates mainly *M. balthica*, *Cerastoderma glaucum* Bruguière and *N. diversicolor* are found in the sediment while *M. edulis* is more abundant in the layer of *F. lumbricalis*. Higher biomass of the polychaete under the mat of *F. lumbricalis* agrees with the hypothesis that uniformity of assemblage facilitates the establishment of introduced species (Carlton 1996). Also, it is likely that a thick mat of *F. lumbricalis* protects infauna effectively from fish predation. On the other hand, intermediate disturbance (Connel 1978) due to possible temporary hypoxia under *F. lumbricalis* may be beneficial for the establishment of opportunistic species such as *M. viridis* (Kotta & Kotta 1998, VI).

As compared to the Latvian side of the Gulf of Riga (Lagzdins & Pallo 1994), the abundances of *M. viridis* in the Estonian coastal sea were rather low, seldom surpassing 100 ind m$^{-2}$. Hence, an increase in the abundances of *M. viridis* is expected in the coming years.

To conclude, the population of *M. viridis* has not yet stabilised in the study area with an exception of the deepest areas of the Gulf of Riga where it has been found at low but constant numbers. The establishment of *M. viridis* has been more successful either in more eutrophicated regions or in more uniform biotopes.

**Habitat selection and grazing pressure of *Idotea baltica***

Invertebrate herbivory is considered a major factor determining the structure and development of macroalgal assemblages (e.g. Paine 1974, Lubchenco 1978, 1982, Hawkins & Hartnoll 1983). On the other hand, the abundance of herbivores is regulated by the competition for food and predation (Menge 1976, Lubchenco & Menge 1978, Edgar 1983, Branch 1984, Holmlund et al. 1990). Hence, the fluctuations in the abundance of herbivores have drastic repercussions on the populations of their competitors, predators and macroalgae (Barnes & Hughes, 1988).

In the Baltic Sea the most prevalent benthic invertebrate herbivore is the marine isopod *I. baltica* (Jansson 1974, Salemaa 1979, Jansson et al. 1982). The species plays an important role in the dynamics of *Fucus serratus* L. and *F. vesiculosus* L. assemblages (Salemaa 1987, Malm 1999). The latter is the
dominant macroalgal species in the Baltic Sea comprising up to 43% of the benthic plant biomass (Kautsky H. 1995).

As a consequence of the rise in the nutritional load the biomass of filamentous algae has considerably increased in the coastal areas (Rosenberg 1985, Hull 1987, Gray 1992, Kolbe et al. 1995). Consequently, the stock of *F. vesiculosus* has diminished or even extinguished in wide areas (Kangas et al. 1982, Plinski & Florczyk 1984, Vogt & Schramm 1991). This decline is attributed to the lower competitiveness of *F. vesiculosus* at higher nutrient concentrations (Pedersen & Borum 1996) and the shading effect of filamentous algae combined with increased herbivory by the isopod *I. baltica* (Kangas et al. 1982, Salemaa 1987, Malm 1999).

Under favourable conditions, such as an outbreak of the filamentous algae *P. littoralis*, high summer temperatures and diminished predation by fish, the density of *I. baltica* may increase rapidly. After eliminating *F. vesiculosus* a dense population of *I. baltica* is expected either to crash or to switch to an alternative diet (II).

During this investigation a major change in the algae-herbivore relationship was observed in Kõiguste Bay. After the outbreak of the filamentous algae *P. littoralis*, the stands of *F. vesiculosus* almost disappeared. At the same time the biomass of *I. baltica* increased a hundredfold and its depth distribution widened considerably. Previously *I. baltica* inhabited *F. vesiculosus* but today it is found mainly within the bushes of *F. lumbricalis* and *P. littoralis* (II).

*I. baltica* consumed larger amounts of *P. littoralis* than *F. lumbricalis*. The grazing values were strongly dependent on the season. The daily consumption of *F. lumbricalis* (mg dw algae per g dw *I. baltica*) varied from 20 mg in July to 3 mg in October. The corresponding values for *P. littoralis* were 49 and 27 mg (II).

Low algal production and high intensity of herbivory resulted in a relatively high grazing pressure of *I. baltica* on *P. littoralis* in July. On the other hand, the grazing pressure on *P. littoralis* was very low during October due to high algal production and lower grazing values. The seasonal differences in the grazing pressure of *I. baltica* on *F. lumbricalis* were not so pronounced as on *P. littoralis*. *I. baltica* consumed up to 2.2% of the net production of *F. lumbricalis* in July and 1.2% in October. The corresponding values for *P. littoralis* were 4.7 and 0.7%, respectively (II).

However, under the experimental conditions *I. baltica* preferred *F. lumbricalis* as a habitat. These results suggest that in Kõiguste Bay the habitat selection of *I. baltica* is driven by both the food quality and the morphology of algae. It is very likely that *F. lumbricalis* offers better refuge from predators whereas *P. littoralis* serves as a better food. The maximum density of *I. baltica* was observed in the shallower areas where the proportion of epiphytic *P. littoralis* on *F. lumbricalis* was the highest. By removing the fast-growing epiphyte, isopods also protect the slow growing *F. lumbricalis* from a “nuisance alga” *P. littoralis* (II).
An advantageous effect of herbivores on the growth of macroalgae has been previously documented (e.g. Brawley & Adey 1981). By favouring the persistence of perennial macrophytes (Lubchenco 1983) herbivores stabilise the benthic community and contribute to the maintenance of diversity. However, as only an insignificant proportion of the production of *P. littoralis* was removed by idoteid grazing, it is likely that the grazing pressure is not sufficient to control the outbreak of *P. littoralis*.

**Grazing impact of Mytilus edulis and Dreissena polymorpha**

*M. edulis* and *D. polymorpha* are the most prevalent filter-feeders on hard bottoms in the north-eastern Baltic Sea (Järvekülg 1979, Kotta & Kotta 1995, Kotta *et al.* 1998a, 1998b, 1999, VI–VIII). Owing to the differences in their salinity preferences, *M. edulis* occur in the areas where salinity is higher than 4 psu (Järvekülg 1979) whereas *D. polymorpha* are traditionally confined at salinities below 5 psu (Järvekülg 1979, Kotta *et al.* 1998b, Kautsky *et al.* 1999, VII).

Except for a few studies, direct estimates of food uptake in bivalves under natural conditions are rare (Kautsky & Evans 1987, Cranford & Hargrave 1994). However, such estimates are essential to validate the proposed role of filter-feeding bivalves in coastal ecosystems (e.g. Cloern 1982). The main focus of this study was to quantify the impact of natural populations of bivalves on the phytoplankton stock rather than to quantify their role in the cycling of matter (Kautsky & Evans 1987) or to study their feeding response and utilisation efficiency of food (Cranford & Hargrave 1994). Hence, we quantified the egestion of the algal constituents, the content of chlorophyll and biogenic silicate (I).

Grazing experiments were carried out in the littoral zone of the Gulf of Riga. The Kõiguste transect represents the northern Gulf of Riga, characterised by a wide coastal zone and moderate densities of *M. edulis* (500 ind m⁻², 50 g dw m⁻²). The Saulkrasti transect is located in the southern Gulf of Riga, adjacent to the Daugava River. The region has a narrow coastal area and supports a dense population of *D. polymorpha* (max 8500 ind m⁻², 1450 g dw m⁻²) (I).

The most important result of this study was the observation that the *in situ* defaecation rate of chloropigments in the bivalves scaled to the ambient concentration of chlorophyll and probably levelled off at high food concentrations. Such a functional response is in line with numerous studies carried out under controlled conditions in the laboratory (e.g. Winter 1978, Bayne *et al.* 1989, Riisgård 1991) and is caused by either a decrease in clearance rate, an increase in the rejection rate of food particles (i.e. pseudofaeces production) at high food concentrations or most likely, a combination of both processes (Kiorboe *et al.* 1980).
When biogenic silicate was used as a tracer for the food the defaecation generally showed a closer coupling to the ambient concentration but without the levelling-off at higher concentrations. The filtration rate when based on biogenic silicate was respectively 6 times and 2 times as high as the rates calculated on the basis of total chlorophyll (chlorophyll \(a + \) phaeopigments) and chlorophyll \(a\). This points to (1) a selective feeding by \(M. \) edulis towards diatoms or (2) an underestimation of the degradation rate of chlorophyll during trap deployment (I).

During spring the defaecation rate of total chlorophyll by \(M. \) edulis was approximately 3 times as high as in July. Assuming an insignificant loss of pigment in the gut at low temperatures in May and correcting for the estimated loss in July the size specific ingestion rates were comparable in the two seasons. The filtration rate and consequently the ingestion rate in mussels increase with temperature (e.g. Jørgensen et al. 1990). Hence, in May at high food concentrations (8–70 \(\mu \)g chlorophyll \(a \) l\(^{-1}\)), the ingestion rate was probably limited by temperature rather than food concentration, while in July at 10 times lower food concentration but at much higher temperature (16°C) the ingestion rate increased gradually with food concentration. Interestingly, the ingestion of algae continued to increase at the increasing algal concentration along with the production of pseudofaeces. This points to an efficient selection process (I).

During spring the egestion rate of \(D. \) polymorpha was comparable to \(M. \) edulis at the Kõiguste transect. Accounting for the low temperature the measured egestion rate in \(D. \) polymorpha was comparable to rates measured in their freshwater habitat (Horgan & Mills 1997). Attempts to estimate the grazing rate of \(D. \) polymorpha in July failed, probably due to the rapidly changing salinity (1–4 psu) caused by the Daugava River plume intercepting the stations several times during trap deployment (I).

Based on the individual grazing rates and bivalve abundance the grazing impact of \(M. \) edulis was estimated at 31–91% of the standing stock of phytoplankton per day in the littoral zone of the northern Gulf of Riga in July. In May the grazing impact was insignificant at 1 to 8% of the phytoplankton stock per day due to high algal biomass and low temperature limiting the filtration rate. During our study in July autotrophic and heterotrophic processes in the water column were in close balance, hence the significant benthic grazing pressure was the major sink for algae in the littoral zone. This was clearly reflected in the strong horizontal and vertical gradients in chlorophyll \(a\) measured during the study (I). Kõiguste Bay has extensive shallow areas and moderate water exchange — features that favour benthic control over phytoplankton (e.g. Officer et al. 1982). The biotopes resembling those of Kõiguste Bay prevail in the north-eastern Baltic Sea (Järvekülg 1979, Kotta & Kotta 1995, Kotta et al. 1999, VII–VIII). Therefore, it is very likely that benthic control of phytoplankton is more commonplace in the more enclosed areas of the Baltic Sea than previously thought.
Effect of the introduced polychaete *Marenzelleria viridis* on the native amphipod *Monoporeia affinis*

The arrival of a new organism may alter the rates of a particular ecosystem functioning or may cause the appearance of an entirely new function. Hence, the biological consequences to the community structure, species interactions, energy flow and evolution can be profound (Mills et al. 1993, Daehler & Strong 1996, Parker et al. 1999).

The studies that have attempted to quantify impacts have often done so in a correlative manner, either comparing one site before and after the invasion or comparing different sites with and without an invader present at the same time. Experimental studies elucidating the mechanisms involved are rare (e.g. Parker et al. 1999, Ruiz et al. 1999).

The greatest impact often occurs when a nonindigeneous species performs an entirely novel function in the recipient community (Simberloff 1991, Ruesink et al. 1995). This is the case for the originally North-American polychaete *M. viridis*. The polychaete is now filling the niche of deep-burrowing deposit-feeders (e.g. Essink & Kleef 1993, Kotta & Kotta 1998) that has previously been empty in the north-eastern part of the Baltic Sea (Bonsdorff & Pearson 1999). The species has become a dominant element in many shallow water ecosystems (e.g. Zettler 1997) and, hence is thought to affect severely the native assemblages (Atkins et al. 1987, Zettler 1996, Essink & Kleef 1993, Olenin & Leppäkoski 1999).

*M. viridis* was found to have a negative effect on the amphipod *M. affinis*. The polychaetes depressed the amphipod length and had a slight negative effect on its weight, but did not affect its survival (III). The results indicated that this was due to competitive interactions for food. All previous evidence we had on the influence of this polychaete on other species both in the Baltic and elsewhere were circumstantial.

The negative effect of *M. viridis* on *M. affinis* was observed at a density of 2000 amphipods m$^{-2}$, which is equivalent to the natural densities found in the study area (Cederwall 1977, Järvekülg 1979, Laine et al. 1997). At higher amphipod densities the effect of *M. viridis* was not statistically significant indicating that intraspecific competition was the main regulatory process in these treatments. Similarly to the findings of Hill (1992) we found that the growth was reduced at higher amphipod densities. However, when amphipods were fed during the experiment, the variation in juvenile length and weight was independent of animal density. The amphipod length was always shorter in the presence of *M. viridis*, indicating interference competition between polychaetes and amphipods (III).

However, the effect of *M. viridis* on *M. affinis* was not so strong as we assumed. Competitive interactions for food between *M. viridis* and *M. affinis* may be severer in the field than shown in this experiment. At least three reasons can
be suggested. (1) We used low densities of polychaetes (200 ind m\(^{-2}\)) whereas the abundances recorded in the Baltic may reach up to 28,000 ind m\(^{-2}\) with an average at 500–1000 ind m\(^{-2}\) (Zettler 1997). (2) The experimental animals were small, though typical for the northern Baltic Sea. (3) Being collected from the shallow and organically enriched area, it is likely that the polychaetes were not fully adapted to cold and oligotrophic conditions of the northern Baltic Sea.

The reduction in the growth of amphipods due to the competitive interactions between *M. viridis* and *M. affinis* is expected to have an effect on the duration of the amphipod’s life cycle, *i.e.* recruitment is prolonged and fecundity is reduced. Consequently, amphipods are exposed to possible predation longer and, hence, population size is likely to be diminished. We expect that the negative effect of *M. viridis* on the population of *M. affinis* will have drastic repercussions on higher trophic levels such as intermediate predators (Haahtela 1990, Hill & Elmgren 1992, Ejdung 1998) and fish species (Aneer 1975, Aarnio *et al.* 1996) that rely on benthic fauna as their food resource. The overall community structure is also likely to change with some species gaining from bioturbating activities of the polychaete while others may reduce in abundance or disappear.
CONCLUSIONS

The type of benthic vegetation was the main factor structuring macrozoobenthos in the coastal sea of the Gulf of Riga and the Väinameri. Nutrient concentrations in water were found to be significant only in the most eutrophicated areas such as Pärnu Bay and the coastal sea adjacent to the Daugava River (Kotta & Kotta 1995, IV, VI–VII).

The species diversity of macrozoobenthos has notably declined both in less and more eutrophicated areas during last decades. Several phytophilous species have become rare in extensive areas while the biomass of filter-feeding mussels has considerably increased (VIII).

Owing to the large filtration capacity, the populations of filter-feeders are able to control the standing stock of pelagic primary producers (Kautsky & Evans 1987, I). Benthic control over phytoplankton is more likely found in areas that are shallow and have moderate water exchange (Officer et al. 1982, I).

The biomass of filamentous algae has significantly increased in the study area during the last five years. As a consequence, *Idotea baltica*, the most prevalent benthic herbivore, has switched into an alternative habitat and diet (II).

Non-indigenous species continue to accumulate in the north-eastern part of the Baltic Sea. However, the knowledge about their ecological impact and interactions with other anthropogenic stressors is still very limited (Leppäkoski 1991, Olenin & Leppäkoski 1999, Kotta 2000, V). Because of their wide distribution area and high biomasses *Dreissena polymorpha* and *Marenzelleria viridis* are considered among the most important exotics in the study area (Kotta et al. 1998b, Kotta & Kotta 1998, V).

The establishment of the exotics has been more successful in more eutrophicated areas or in more uniform biotopes (Kotta et al. 1998b, V–VII). In these areas *D. polymorpha* has an important role as a linking organism between the pelagic and benthic systems (I).

*M. viridis* has a potential to reduce the growth of the native amphipod *Monoporeia affinis* due to the competitive interactions for food. As a consequence the amphipod’s recruitment is likely to be prolonged, fecundity to be reduced and, hence, population size to diminish (III).
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ABSTRACT

During May and June of 1966, the grazing impact of the oyster drill (Ocenebra erinacea) on the photosynthetic productivity of marine diatoms and peridinin algae in the Gulf of Maine was measured. Two methods were used.

1. Grazing by 0.1 cm³ samples of both the oyster drill and the autochthonous diatom flora was determined in the laboratory, with the use of plaque technique.

2. Grazing in situ was followed by collecting samples of diatom assemblages in bottles of 1,500 ml capacity and comparing the number of individuals with and without the presence of oysters. Following this experiment, the number of peridinin algae was determined in the same assemblages and compared with data from a previous experiment in which the number of individuals was determined in the absence of the organisms.
Kotta, J. & Møhlenberg, F.
Grazing impact of *Mytilus edulis* L. and *Dreissena polymorpha* (Pallas) in the Gulf of Riga, Baltic Sea estimated from biodeposition rates of algal pigments and biogenic silicate (submitted to *Ophelia*).
GRAZING IMPACT OF *MYTILUS EDULIS* L. AND *DREISSENA POLYMORPHA* (PALLAS) IN THE GULF OF RIGA, BALTIC SEA ESTIMATED FROM BIODEPOSITION RATES OF ALGAL PIGMENTS AND BIOGENIC SILICATE

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ABSTRACT

Grazing rates of *Mytilus edulis* and *Dreissena polymorpha* were estimated in the Gulf of Riga during May and July 1996. The faecal material was quantified by using chlorophyll and biogenic silica (BSi) as tracers for planktonic algae. Faeces production rate of *M. edulis* (shell length: 20 mm) ranged between 0.05 and 0.37 μg Chl *a* equivalent ind−1 h−1 depending on season and ambient chlorophyll concentration. Faeces production rate of *D. polymorpha* during the spring bloom in May varied between 0.23 and 0.4 μg Chl *a* equivalent ind−1 h−1. In July faeces production in *M. edulis* increased gradually with ambient biogenic silicate from 2.0 to 7.4 μg BSi ind−1 h−1. After correcting for loss of fluorescent material during gut passage (loss: 61%) the population grazing impact in July was estimated at 9–36% d−1 of the chlorophyll stock in the littoral zone. Grazing impact calculated in terms of biogenic silicate was much higher at 95% d−1. During the spring bloom in May the population of bivalves consumed less than 4% of the algal stock. A high grazing impact by *M. edulis* in the coastal zone during summer was supported by strong horizontal and vertical gradients in chlorophyll. Hence, the populations of benthic suspension feeders in the littoral zone of the Gulf of Riga constitute an important sink for primary production, especially during summer.

INTRODUCTION

Suspension feeders such as mussels, clams and tunicates often dominate the macrofaunal communities in shallow coastal waters. Because of their large filtration capacity such populations are theoretically able to filter major parts of the water column each day (Riisgård & Møhlenberg 1979), and thereby via grazing directly control the standing stock of pelagic primary producers. Traditionally, the impact of benthic suspension
feeders on plankton has been calculated combining laboratory derived filtration rates with field estimates of population densities (e.g. Cloern 1982, Nichols 1984, Loo & Rosenberg 1989, Petersen & Riisgård 1992). However, also field studies have shown that dense populations of suspension-feeding bivalves can deplete the overlaying water of algae (Wright et al. 1982, Fréchette et al. 1989, Asmus & Asmus 1991, Peterson & Black 1991, Muschenheim & Newell 1992). In dense bottom cultures, for example, depletion of algae can occur within meters of the leading edge of a mussel bed (Newell et al. 1989). In situ studies quantifying broad-scale effects of evenly dispersed and less dense bivalve populations are scarce, however, and usually they are based on indirect evidence and modelling approaches (e.g. Cloern 1982, Møhlenberg 1995).

Phytoplankton is considered to be the prime food for benthic filter feeders. Therefore, the content of phytoplankton pigments in benthic filter feeders has previously been used to assess food availability in situ (Jensen & Sakshaug 1970a,b, Ansell 1974a,b, Mann 1977, Christensen & Kanneworff 1985, Kamermans 1993, Josefson et al. 1995). However, the gut residence time of 1–2 hours in mussels (Kiorboe et al. 1980) makes studies with weekly–monthly sampling intervals unsuitable for assessing the temporal variation in the feeding of suspension feeding benthos. This problem was overcome by Kautsky and Evans (1987) and later by Cranford and Hargrave (1994) by applying an in situ trap technique to quantify the rate of biodeposition in *Mytilus edulis* L. and *Placopecten magellanius* (Gmelin), respectively.

In this study we adopted a similar approach to estimate the grazing rates of the dominant suspension-feeders, *M. edulis* and *Dreissena polymorpha* (Pallas) in the Gulf of Riga, Baltic Sea. However, in contrast to these previous studies, which quantified biodeposition in terms of carbon and nutrients, we chose chlorophyll and biogenic silicate as a proxy for planktonic algae and diatoms, respectively, to calculate the grazing impact on the algal community.

**MATERIAL AND METHODS**

Environmental setting: The study was carried out on two transects in the littoral zone of the Gulf of Riga in May and August 1996 (Fig. 1). One transect was located in Estonian coastal waters (Kõiguste Bay) characterised by a wide coastal zone with a diverse bottom topography and extensive reaches of boulders. In the shallower areas boulders were covered by *Pilayella littoralis* Kjellm. (coverage 100%) and *Fucus vesiculosus* L. (25%) and in the deeper area by *P. littoralis* (100%). A scattered population of *M. edulis* occurred on the boulders.

At the Saulkrasti transect coarse sandy bottom prevailed down to a depth of 4 m. At greater depths sand was replaced by boulders (coverage 75%) and stones (25%). The boulders were practically devoid of vegetation but housed a dense population of *D. polymorpha*. The transect is located close to the mouth of the Daugava River and depending on meteorological conditions the river plume regularly reaches the transect (Stålnacke et al. 1999, Tamminen & Seppälä 1999).

Experimental: The abundance and biomass of bivalves were estimated along the transects. Samples were collected by divers using 20×20 and 40×40 cm frames placed randomly at a location. All bivalves within the frame were collected. The length of the bivalves was measured to the nearest 0.1 mm using vernier calipers. Shell (SDW) and
shell-free dry weights (SFDW) were determined after drying the individuals at 60°C for 48 hours. At least 60 individuals in a sample were randomly selected and analysed.

The grazing rates of the dominant suspension feeders, *M. edulis* and *D. polymorpha*, were estimated by quantifying the egestion of total chlorophyll and biogenic silicate by the individuals deployed *in situ* at 2 and 5 m depth at the transects. Bivalves of 13–28 mm shell length were collected by diver in the vicinity of deployment. Three individuals were placed on the net of the funnel allowing biodeposits to sediment to the collecting vial below (Fig. 2). Four replicates were used at each station. Biodeposits were retrieved after 12 h incubation (8:00–20:00; 20:00–8:00). At each station, 4 and 6 incubations were carried out in spring and summer, respectively. During deployment the temperature was monitored continuously using EBRO loggers that record data every 10 min. After deployment the shell lengths were recorded, the sedimented material in the vials was sorted under a dissecting microscope, faeces were collected with a pipette and filtered on Whatman CF/C filters within 4 h of retrieval. Filters were extracted in 96% ethanol overnight. Chlorophyll *a* was quantified fluorometrically correcting for phaeopigments (Pha) (Strickland & Parsons 1972). The values of chlorophyll *a* equivalent or total chlorophyll (Chi *a* eq) were calculated as Chi *a* eq = Chi *a* + 1.52 * Pha. During summer, faeces samples were split in two after sorting and one subsample was analysed for chlorophyll and the other for biogenic silicate (Conley & Johnston 1995).

Water for chlorophyll and biogenic silicate (summer only) was sampled by divers using 0.5 l screw cap flasks. Care was taken not to resuspend particulate material during sampling. Samples were taken within 25 cm from the cages in connection with retrieving biodeposits (i.e. every 12 h). Hence, the average concentration of chlorophyll sampled at the start and end of an incubation was used as a measure of food concentration during incubation. Biogenic silicate was analysed in the samples taken in the beginning of deployment. Filtration and extraction of these samples were carried out within 1 h after sampling. The water samples were filtered onto Whatman GF/F filters. Samples were extracted in 96% ethanol overnight. The contents of Chi *a* and Pha were measured fluorometrically (Strickland & Parsons 1972).

In order to estimate the loss of chlorophyll during gut passage a separate experiment was carried out in summer. Thirty mussels were placed in an aquarium filled with filtered seawater and left there for 24 h to allow bivalves to empty their guts. The aquarium was submerged in running surface water to keep the temperature at ambient level. After 24 h the filtered water was replaced by 8 l of seawater sampled at 3 m depth. During the following 15 h faeces were collected every second hour along with water samples for the measurement of chlorophyll. The experiment was finished when the mussels stopped to produce faeces. The loss of chlorophyll during gut passage was estimated as: $L = \text{tot Chl}_{ws} - \text{tot Chl}_{we} - \sum \text{tot Chl}_f$, where tot Chl<sub>ws</sub> and tot Chl<sub>we</sub> are the suspended total chlorophyll content in the aquarium at the start and end of the incubation, respectively, and $\sum \text{tot Chl}_f$ is the chlorophyll content in the faeces produced during the incubation. In addition, loss of chlorophyll due to sedimentation was estimated in a control aquarium without mussels.

Unfortunately we did not perform similar experiments during spring. However, previous experiments carried out at 5°C have shown that the pigment loss during gut passage in *M. edulis* was less than 6% (Møhlenberg, unpublished).
RESULTS

Along the Kõiguste transect the abundance and biomass of *M. edulis* varied little within the depth interval of 1.5–5 m, being on average 600 ind m\(^{-2}\) and 6 g dry wt of soft parts m\(^{-2}\), respectively (Fig. 3). At the Saulkrasti transect a very high abundance (= 8000 ind m\(^{-2}\)) and biomass (>100 g dry wt of soft parts m\(^{-2}\)) of *D. polymorpha* were confined to the depth interval of 5–7 m.

The measured rates of faeces production, temperature and ambient concentration of chlorophyll and biogenic silicate are shown in Table 1. In May at a high ambient chlorophyll concentration and low temperatures the rates varied between 0.20 and 0.37 µg tot chlorophyll ind\(^{-1}\) h\(^{-1}\) at the Kõiguste transect (*M. edulis*) and between 0.23 and 0.40 µg tot chlorophyll ind\(^{-1}\) h\(^{-1}\) at the Saulkrasti transect (*D. polymorpha*). In July, at a lower ambient concentration of total chlorophyll (2.6–6.5 µg L\(^{-1}\)), the faeces production rate varied between 0.037 and 0.16 µg tot chlorophyll ind\(^{-1}\) h\(^{-1}\) in *M. edulis* at the Kõiguste transect. During summer the defaecation rate increased with ambient concentration of chlorophyll \(\alpha\), total chlorophyll and biogenic silicate (Fig. 4). Fitted functions suggested a satiation of defaecation rate when measured in terms of chlorophyll even though a linear relation gave almost identical correlation coefficients (\(R^2 = 0.39–0.40\)). The relationship between the water concentration and the defaecation rate of biogenic silicate was best described by a linear function (Fig. 4C). In Table 2 the slopes of the linear parts of the functional-response curves are presented. In the case of an inert (i.e. non-degradable) substance the slopes represent the filtration rate ranging from 0.06 to 0.89 l h\(^{-1}\) for a standard individual.

The temporal variation in the chlorophyll content (i.e. the concentration times aquarium volume) and accumulated defaecation rate during the budget experiment is shown in Fig. 5. After 3 h most of the phytoplankton (i.e. chlorophyll) had disappeared and the defaecation rate began to decrease. The initial decrease in chlorophyll \(\alpha\) in water was similar to that of phaeopigments. However, from 9 to 15 hours the concentration of phaeopigments increased steadily (0 → 0.10 µg L\(^{-1}\)), probably due to leakage from faeces, while the concentration of chlorophyll \(\alpha\) remained low. The loss in terms of total chlorophyll during the experiment amounted to 61.4%. Taking this loss into account the filtration rates based on chlorophyll increased to 0.15 and 0.45 l ind\(^{-1}\) h\(^{-1}\) for Chl \(\alpha\) eq and Chl \(\alpha\), respectively (Table 3).

Algal grazing by the mussel population in July was estimated from the functional relations (Fig. 4, Table 3) after correction for loss of chlorophyll during gut passage and taking into account the data on mussel abundance and size distribution. For May we used the average defaecation rate throughout the depth range as a measure for ingestion in combination with abundance/size distribution to calculate the population grazing rate. Grazing by individuals of different size (\(G_i\)) was scaled by shell length, i.e. \(G_i = G_{20} \times l^2/20^2\), where \(G_{20}\) is the grazing rate of 20 mm individuals and \(l\) the shell length (Kiorboe & Møhlenberg 1981).

For the Kõiguste transect the ambient concentration at 3 m depth was calculated by linear interpolation between 2–5 m, assuming that concentrations at 1.5 m and 2 m were identical. At Kõiguste the population grazing rate showed only a minor variation along the transect in accordance with the horizontal distribution of mussels and insignificant variation between seasons (Fig. 6A–C). Along the Saulkrasti transect the grazing rate peaked at 6–7 m reflecting the high abundance in this region (Fig. 6D). The grazing impact on the standing stock of phytoplankton was low in May, varying between 1 and
8% d⁻¹. In July the grazing impact was much higher at 8.5 or 31.4% depending on whether total chlorophyll or chlorophyll a was used as the measure for available food in water. Alternatively, if the calculation was based on biogenic silicate the grazing impact was much higher at 91% of diatom stock per day (Fig. 6B&C).

DISCUSSION

The most important result of this study is the observation that the in situ defaecation rate of chloropigments in the bivalves scales to ambient concentration of chlorophyll and probably levels off at high food concentrations. Such a functional response is in line with numerous studies carried out under controlled conditions in the laboratory (e.g. Winter 1978, Bayne et al. 1989, Riisgård 1991) and is caused by either a decrease in the clearance rate, an increase in the rejection rate of food particles (i.e. pseudofaeces production) at high food concentrations or most likely, a combination of both processes (Kiorboe et al. 1980). Except for a few studies direct estimates of food uptake in bivalves under natural conditions are rare (Kautsky & Evans 1987, Cranford & Hargrave 1994); however, such estimates are essential to validate the proposed role of filter feeding bivalves in coastal ecosystems (e.g. Cloern 1982). In the natural environment hydrodynamic constraints, sediment load, temporal variation in food concentration and quality vary and act in concert with behavioural variation in filtering activity of the mussels, hence the realized rate of grazing is likely to deviate from laboratory estimates. In contrast to the previous studies our main focus was to quantify the impact of a natural population of bivalves on the phytoplankton stock rather than to quantify their role in the cycling of matter (Kautsky & Evans 1987) or study their feeding response and utilisation efficiency of food (Cranford & Hargrave 1994). To that end we quantified the egestion of the algal constituents chlorophyll and biogenic silicate. As has been pointed out repeatedly, especially in studies dealing with the grazing in copepods, pigment loss during gut passage is highly variable and should preferably be quantified on each study occasion (e.g. Penry & Frost 1991). The few published studies in bivalves also indicate a significant breakdown of chlorophyll during gut passage even though pigment budgets have not been presented (Hawkins et al. 1986, Pastoureaud et al. 1996). In addition, intermittent accumulation of phaeopigments in the digestive gland for up till weeks further will complicate the interpretation of results (Redden et al. 1993). In this study the chlorophyll loss was estimated at 61%. This loss is markedly higher than estimated for M. edulis from a Danish estuary using a similar set-up (Møhlenberg in prep.). As evidenced for copepods the previous feeding history and food composition can affect the loss of pigments during gut passage (Penry & Frost 1991). We suggest that individual variation in chlorophyll degradation and temporal storage of pigments are partly responsible for the large variation in the relations of functional response (see Fig. 4).

When biogenic silicate was used as the tracer for food the defaecation generally showed a closer coupling to ambient concentration but without the levelling-off at higher concentrations. However, biogenic silicate is a natural constituent of diatoms and has previously been used to estimate the assimilation rate of carbon in copepods under the assumption that BSi acts as an inert marker (Tande & Slagsted 1985). In this study the filtration rate when based on biogenic silicate was 6 times and 2 times as high as the rates calculated on basis of Chl a eq and Chl a, respectively. This points to (1) selective
feeding by *M. edulis* towards diatoms or (2) underestimation of the loss of chlorophyll during trap deployment. Neither process can be ruled out. In July Chl a constituted on average less than 30% of chloropigments (Table 1), indicating dominance of particles of low nutritional quality. We did not attempt to quantify pseudofaeces, however, trays with live mussels consistently collected more debris than a control tray with 3 empty shell pairs. Therefore, we conclude that production of pseudofaeces occurred, which is a prerequisite for particle selection to take place (Foster-Smith 1975, Kiorboe & Møhlenberg 1981). An additional possible error is related to particle size. *M. edulis* efficiently retains particles above 3—4 μm (Møhlenberg & Riisgård 1978), but becomes increasingly “leaky” at smaller particle sizes. Therefore, if nanoplankton retained by the GF/F filters (pore size = 1 μm) constituted a significant part of chlorophyll the food available to the mussels would have been overestimated when determined in terms of chlorophyll but not in terms of BSi due to the larger size of diatoms. Unfortunately, we do not have substantial information to qualify this further. An additional bias may result from the different sampling schemes of faeces *in situ* (interval 12 h) and in the budget experiment (2 h). Hence, if degradation of chlorophyll in faeces continued after egestion the fraction lost would be higher in the traps than in the aquarium experiment. Therefore, filtration rates based on chlorophyll are likely to represent very conservative estimates. To conclude, calculated filtration from measured rates of egestion of chloropigments and BSi showed rates (Chl: 0.45 l·h⁻¹, BSi: 0.89 l·h⁻¹) that were lower but still comparable to the filtration rate predicted from Kiorboe & Møhlenberg (1981) for individuals of identical size.

During spring the defaecation rate of Chl a eq in *M. edulis* was approximately 3 times as high as in July (Table 1). Assuming an insignificant loss of pigment in the gut at low temperatures in May and correcting for the estimated loss in July the size specific ingestion rates were comparable in the two seasons. Filtration rate and consequently ingestion rate in mussels increase with temperature (e.g. Jørgensen et al. 1990). Hence, in May at a high food concentration (8—70 μg Chl a l⁻¹) the ingestion rate was probably limited by temperature rather than by food concentration, while in July at 10 times lower food concentration but at much higher temperature (16°C) the ingestion rate increased gradually with food concentration (Fig. 4). Interestingly, the ingestion of algae continued to increase at increasing algal concentration along with the production of pseudofaeces. This points to an efficient selection process.

*D. polymorpha* attained a very high abundance at the Saulkrasti transect in the southern Gulf of Riga. The salinity regime here (i.e. 4—5 psu) is close to the upper tolerance limit of the species (Järvekülg 1979). Still, during spring the egestion rate was comparable to that of *M. edulis* at the northern transect. Accounting for the low temperature the measured egestion rate in *D. polymorpha* was comparable to rates measured in their freshwater habitat (Horgan & Mills 1997). In July attempts to estimate the grazing rate in *D. polymorpha* failed, probably due to rapidly changing salinity (1—4 psu) caused by the Daugava plume intercepting the stations several times during our occupation of the transect.

Based on the individual grazing rates and bivalve abundance the benthic grazing impact in the littoral zone at the Kõiguste transect was estimated at 31—91% of the standing stock of phytoplankton per day in July. In May the grazing impact was insignificant at 1 to 8% of the phytoplankton stock per day due to high algal biomass and low temperature limiting the filtration rate. During our study in July autotrophic and heterotrophic processes in the water column were in close balance (Møhlenberg in
pre), hence the significant benthic grazing pressure was the major sink for algae in the littoral zone. This was clearly reflected in the strong horizontal and vertical gradients in chlorophyll a measured during the study (Fig. 7). Kõiguste Bay has extensive shallow areas and moderate water exchange — features that favour benthic control over phytoplankton (e.g. Officer et al. 1982). Biotopes resembling those of Kõiguste Bay prevail in the northeastern Baltic Sea (Järvekülg 1979, Kotta & Kotta 1995, Kotta & Kotta 1997, Kotta et al. 1999). Therefore, it is very likely that benthic control of phytoplankton in the littoral zone is more commonplace in the Baltic Sea than previously thought. Hence, we may assume that phytoplankton dynamics is strongly coupled with benthic processes in these areas.

REFERENCES


Christensen, H. & E. Kanneworff 1985. Sedimenting phytoplankton as major food source for suspension and deposit feeders in the Øresund. — Ophelia 24: 223–244.


Table 1. Ambient conditions during incubations in May and July 1996; faeces production rates, FP calculated for a standard size bivalve (shell length = 20 mm; i.e. $FP_{20} = FP_{*} \times 20^{2/\ell^2}$)

<table>
<thead>
<tr>
<th>Transect</th>
<th>Date</th>
<th>Hours</th>
<th>Depth m</th>
<th>Temp °C</th>
<th>Salinity ppt</th>
<th>Chl $a$ $\mu$g L$^{-1}$ start-end</th>
<th>Chl $a$ eq $\mu$g L$^{-1}$ start-end</th>
<th>BSi $\mu$g L$^{-1}$</th>
<th>Shell length mm range</th>
<th>Sample n</th>
<th>Faeces production $\mu$g Chl $a$ eq ind$^{-1}$ h$^{-1}$</th>
<th>$\mu$g BSi ind$^{-1}$ h$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kõiguste</td>
<td>9–10 May</td>
<td>16:00–8:00</td>
<td>2</td>
<td>6.1</td>
<td>5.4</td>
<td>16.0–11.3</td>
<td>17.1–15.7</td>
<td>15–21</td>
<td>4</td>
<td></td>
<td>0.202</td>
<td>0.075</td>
</tr>
<tr>
<td>9–10 May</td>
<td>16:00–8:00</td>
<td>5</td>
<td>6.3</td>
<td>5.5</td>
<td>14.4–13.4</td>
<td>19.1–19.4</td>
<td>13–18</td>
<td>7</td>
<td>0.369</td>
<td>0.225</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-May</td>
<td>8:00–21:00</td>
<td>2</td>
<td>5.9</td>
<td>5.5</td>
<td>11.3–9.0</td>
<td>15.7–14.3</td>
<td>16–19</td>
<td>4</td>
<td>0.266</td>
<td>0.082</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-May</td>
<td>8:00–21:00</td>
<td>5</td>
<td>5.9</td>
<td>5.5</td>
<td>13.4–8.1</td>
<td>19.4–24.7</td>
<td>13–16</td>
<td>6</td>
<td>0.301</td>
<td>0.144</td>
<td></td>
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<tr>
<td>10–11 May</td>
<td>21:00–9:00</td>
<td>2</td>
<td>5.2</td>
<td>5.5</td>
<td>9.0–11.4</td>
<td>14.3–18.6</td>
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<td>0.209</td>
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<tr>
<td>10–11 May</td>
<td>21:00–9:00</td>
<td>5</td>
<td>5.3</td>
<td>5.5</td>
<td>8.1–15.3</td>
<td>24.7–21.0</td>
<td>13–16</td>
<td>3</td>
<td>0.294</td>
<td>0.202</td>
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<td>Saulkrasti</td>
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<td>21:00–9:00</td>
<td>2</td>
<td>3.6</td>
<td>4.77</td>
<td>35.2–43.5</td>
<td>45.2–62.7</td>
<td>13–15</td>
<td>7</td>
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<tr>
<td>13–14 May</td>
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<td>5</td>
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<td>5.20</td>
<td>43.5–50.3</td>
<td>58.9–58.3</td>
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<td>8</td>
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<tr>
<td>14 May</td>
<td>9:00–21:00</td>
<td>2</td>
<td>5.9</td>
<td>4.92</td>
<td>43.5–71.3</td>
<td>62.7–104.0</td>
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<td>7</td>
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<td>0.361</td>
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<tr>
<td>14 May</td>
<td>9:00–21:00</td>
<td>5</td>
<td>5.5</td>
<td>5.05</td>
<td>50.3–60.8</td>
<td>58.3–74.1</td>
<td>16–18</td>
<td>8</td>
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<td>0.106</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kõiguste</td>
<td>23–24 July</td>
<td>20:00–8:30</td>
<td>2</td>
<td>16.2</td>
<td>5.8</td>
<td>1.2–1.9</td>
<td>3.1–4.1</td>
<td>23–28</td>
<td>7</td>
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<td>23–24 July</td>
<td>21:00–9:10</td>
<td>5</td>
<td>15.9</td>
<td>5.7</td>
<td>2.5–2.0</td>
<td>6.5–5.5</td>
<td>7.9</td>
<td>21–24</td>
<td>8</td>
<td>0.160</td>
<td>0.043</td>
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</tr>
<tr>
<td>24 July</td>
<td>8:30–20:45</td>
<td>2</td>
<td>16.4</td>
<td>5.8</td>
<td>1.9–1.0</td>
<td>4.1–2.6</td>
<td>3.9</td>
<td>24–28</td>
<td>4</td>
<td>0.056</td>
<td>0.013</td>
<td></td>
</tr>
<tr>
<td>24–25 July</td>
<td>20:45–7:30</td>
<td>2</td>
<td>16.2</td>
<td>5.7</td>
<td>1.0–1.4</td>
<td>2.6–3.2</td>
<td>3.5</td>
<td>24–28</td>
<td>4</td>
<td>0.037</td>
<td>0.021</td>
<td></td>
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<tr>
<td>25 July</td>
<td>7:30–20:00</td>
<td>2</td>
<td>16.5</td>
<td>5.7</td>
<td>1.4–1.4</td>
<td>3.2–3.5</td>
<td>4.5</td>
<td>24–28</td>
<td>4</td>
<td>0.087</td>
<td>0.022</td>
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<tr>
<td>25–26 July</td>
<td>20:00–8:20</td>
<td>2</td>
<td>16.1</td>
<td>5.7</td>
<td>1.4–1.1</td>
<td>3.5–2.9</td>
<td>4.4</td>
<td>23–26</td>
<td>4</td>
<td>0.103</td>
<td>0.060</td>
<td></td>
</tr>
<tr>
<td>25–26 July</td>
<td>20:30–8:45</td>
<td>5</td>
<td>16.2</td>
<td>5.7</td>
<td>1.4–1.6</td>
<td>3.4–4.3</td>
<td>4.5</td>
<td>23–26</td>
<td>4</td>
<td>0.093</td>
<td>0.068</td>
<td></td>
</tr>
<tr>
<td>26 July</td>
<td>8:20–20:15</td>
<td>2</td>
<td>16.3</td>
<td>5.7</td>
<td>1.1–1.9</td>
<td>2.9–5.1</td>
<td>5.0</td>
<td>23–25</td>
<td>4</td>
<td>0.128</td>
<td>0.039</td>
<td></td>
</tr>
<tr>
<td>26 July</td>
<td>8:45–20:30</td>
<td>5</td>
<td>16.4</td>
<td>5.7</td>
<td>1.6–2.0</td>
<td>4.3–4.8</td>
<td>5.5</td>
<td>23–26</td>
<td>5</td>
<td>0.139</td>
<td>0.054</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Kõiguste transect in July. Slope and intercept of the linear regressions between defaecation rate \((Y, \mu g \text{ Chl} a \text{ eq ind}^{-1} \text{ h}^{-1}, \mu g \text{ BSi ind}^{-1} \text{ h}^{-1})\) and ambient concentration of food \((X, \mu g \text{ Chl} a \text{ l}^{-1}, \mu g \text{ Chl} a \text{ eq l}^{-1}, \mu g \text{ BSi l}^{-1})\). For chlorophyll defaecation only the initial linear part of the relation is included (i.e. ambient Chl \(a < 2 \mu g \text{ l}^{-1}\); ambient Chl \(a \text{ eq} < 4 \mu g \text{ l}^{-1}\)). The slope of the regression between calculated grazing rate and ambient concentration of chlorophyll is shown in brackets.

<table>
<thead>
<tr>
<th>Y</th>
<th>X</th>
<th>Slope ± SD, p-level</th>
<th>Intercept ± SD, p-level</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chl (a) eq defaecation (Chl (a) grazing)</td>
<td>Chla</td>
<td>0.173 ± 0.052, 0.002</td>
<td>-0.177 ± 0.081, 0.04</td>
<td>0.27</td>
</tr>
<tr>
<td>Chl (a) eq defaecation (Chl (a) eq grazing)</td>
<td>Chl (a) eq</td>
<td>0.059 ± 0.015, &lt;0.001</td>
<td>-0.127 ± 0.059, 0.04</td>
<td>0.31</td>
</tr>
<tr>
<td>BSi defaecation</td>
<td>BSi</td>
<td>0.885 ± 0.145, &lt;0.0001</td>
<td>-0.847 ± 0.830, 0.31</td>
<td>0.52</td>
</tr>
</tbody>
</table>

Table 3. Estimated grazing impact by *Mytilus edulis* (Kõiguste) and *Dreissena polymorpha* (Saulkrasti) within the coastal range of mussel occurrence. Impact calculated on the basis of the content of total chlorophyll (Chl \(a\) eq), chlorophyll \(a\) (Chl \(a\)) and biogenic silicate (BSi) in water.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Average grazing impact</th>
<th>% Chl (a) eq d(^{-1})</th>
<th>% Chl (a) d(^{-1})</th>
<th>% BSi d(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kõiguste (0–5 m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>2.4</td>
<td>3.5</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>8.5</td>
<td>31.4</td>
<td>96</td>
</tr>
<tr>
<td>Saulkrasti (0–9 m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>2.0</td>
<td>2.5</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Study area. Arrows indicate the location of transects. Solid line in the graphs show biomass distribution (g dry weight m$^{-2}$) and dotted line abundance distribution (ind m$^{-2}$) of *M. edulis* (at Kõiguste) and *D. polymorpha* (at Saulkrasti) by depth.
Figure 2. Experimental cage used for the measurement of biodeposition rates of the mussels.

Figure 3. Population length-frequency distribution of *M. edulis* (broken line) and *D. polymorpha* (solid line) in the Gulf of Riga during 1996.
Figure 4. Defaecation rate in *Mytilus edulis* at Kõiguste in July as a function of ambient concentration of chlorophyll *a* (A), total chlorophyll *a* (B) and biogenic silicate (C). Each value represents the defaecation rate of 3 individuals. Equations of fitted functions are shown.
Figure 5. Temporal variation of total chlorophyll content in water and accumulated defaecation of total chlorophyll during budget experiment. The loss amounted to 61.4% after 9–15 hours of incubation.

Figure 6. Population grazing rate (bars) and grazing impact (line) on the standing stock of chlorophyll $a$ and biogenic silicate of the mussel population. A: Kõiguste May; B: Kõiguste July; C: Kõiguste July; D: Saulkrasti May. Standing stocks of chlorophyll were obtained from depth integrated samples taken daily at 2, 5 and 10 m stations (Mohlenberg unpubl.).
Figure 7. Spatial distribution of chlorophyll $a$ in the littoral zone of Kõiguste in July. Bottom values from Table 1. Surface values were obtained from a synoptic study (Mohlenberg unpubl.). Average concentration and SD shown.
MAJOR CHANGES IN THE MACROALGAL COMMUNITY COMPOSITION EFFECT THE FOOD AND
HABITAT REQUIREMENT OF JUVENILE SALMON

INTRODUCTION

Riparian to the once untouched of Robinson River. We took certain
nitrogen blooms. We observed that, under normal conditions in the
Cape York Peninsula, nitrogen fixation by plants was significant in
the riparian zone. However, we found that when conditions are
erratic or stressful, nitrogen fixation by plants is dramatically
reduced.

In summary, we observed a decrease in nitrogen fixation
by plants in the riparian zone when conditions are
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Keywords: Riparian habitat, riparian, nitrogen fixation

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At the first opportunity of the Fraser River changed its direction absolutely
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Kotta, J., Paalme, T., Martin, G. & Mäkinen, A. 
Major changes in the macroalgae community composition affect the food and habitat preference of *Idotea baltica*. *Int. Rev. Hydrobiol.* (in press)
MAJOR CHANGES IN THE MACROALGAE COMMUNITY COMPOSITION AFFECT THE FOOD AND HABITAT PREFERENCE OF IDOTEA BALTICA

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\section*{ABSTRACT}

Followed by the massive increase in the biomass of Pilayella littoralis, Fucus vesiculosus almost disappeared from Kõiguste Bay, north-eastern Baltic Sea, during 1995–98. Consequently, Idotea baltica, which previously fed on Fucus, switched to new food items — Furcellaria lumbricalis and Pilayella littoralis. Idotea grazed more on Pilayella than Furcellaria whereas Furcellaria was highly preferred as a habitat. A maximum of 2.2\% and 4.7\% of the production of Furcellaria and Pilayella were removed by grazing. We conclude that the grazing pressure by Idotea is not sufficient to control the outbreak of Pilayella. However, Idotea has an advantageous effect on the persistence of Furcellaria by preferentially removing the fast growing epiphyte Pilayella.

Keywords: Fucus, Furcellaria, grazing, Idotea, Pilayella

* to whom correspondence should be sent

\section*{1. INTRODUCTION}

\textit{Fucus vesiculosus} L. is the dominant macroalgal species in the Baltic Sea comprising up to 43\% of the benthic plant biomass (Kautsky and Kautsky, 1995). In recent years the biomass of the species has notably diminished at many localities (\textit{e.g.} Kangas et al., 1982; Rönberg et al., 1985; Salemaa, 1987; Vogt and Schramm, 1991). This decline was attributed to the lower competitiveness of \textit{F. vesiculosus} at higher nutrient concentrations (Pedersen and Borum, 1996) and the shading effect by filamentous algae combined with increased herbivory by Idotea baltica (Pallas) (Kangas et al., 1982; Salemaa, 1987).

As the first symptoms of the \textit{Fucus} decline appeared the density of Idotea increased explosively. In the latest stages of the succession Idotea concentrated on the weakened plants and due to overgrazing caused the final destruction of the \textit{Fucus} belt (Kangas et al. 1982; Malm, 1999). In some instances macroalgal communities did not return to the
initial stage and the density of idoteids remained high (MALM, 1999; this study). This suggests that *Idotea* may switch to an alternative diet at low biomass of *Fucus*.

In this paper the changes in the algae–herbivore relationships are examined during the notable expansion of *Pilayella littoralis* Kjellm. in Köiguste Bay in 1995–98. We investigated experimentally the habitat selection and grazing pressure of *Idotea baltica* in *Fucus* ousted communities. The results of the experiments are extrapolated to the field in order to elucidate the role of *Idotea* in structuring *Pilayella* dominated macroalgal communities.

2. MATERIAL AND METHODS

**Study area.** Köiguste Bay (Fig. 1) is typified by a wide coastal zone with a diverse bottom topography and macrophyte community. Boulders predominate in the areas shallower than 3 m, pebbles at 3–8 m depth and clay bottoms mixed with gravel and pebbles in deeper areas. Depending on the water exchange between the Gulf of Riga and the Baltic Proper, salinity in Köiguste Bay ranges from 6 to 7 psu. The region is ranked among one of the least eutrophied ones in the Estonian coastal sea (SUURSAAR, 1995).

**Distribution of benthos.** The biomass structure of the benthic communities was described along a transect. The transect was located perpendicularly to the shoreline. Along the transect three replicate samples (20 × 20 cm) were taken by a SCUBA diver in each phytobenthos belt in 1995 and 1998. Macrozoobenthos samples were collected between 0.1 and 8 m by a Tvärminne sampler (KANGAS, 1972) on soft substrate or a suction sampler (HISCOCK and HOARE, 1973) on boulders and limestone. The catching area of both samplers is 314 cm². Three samples were taken from the same site where macrophytobenthos samples were taken. All samples were deep frozen. The material was sorted to species in the laboratory. Animals were counted. Each species was dried separately at 60°C for 3 days and weighed to the nearest of 0.5 mg.

**Production experiments.** Based on the earlier observations *Pilayella* has two clear production maxima in the study area: March–April and August–October. The main productive season of *Furcellaria lumbricalis* J. V. Lamour is between April and August (unpublished data). In the present study the production of *Pilayella* and *Furcellaria* was investigated in July and October. Hence, July represents the season of slow growth for *Pilayella* and fast growth for *Furcellaria* and October vice versa.

*Furcellaria* and *Pilayella* were collected by a diver at 2–4 m depth in Köiguste Bay. The *in situ* diurnal primary production of the species was measured at the end of July and October 1998. Small tufts (ca. 0.05 g dw) with no macroepiphytes and grazers were placed in 600 ml glass bottles, filled with sea water and incubated horizontally on special trays at 0.5 m depth. Bottles that did not include the algae served as the controls. There were five replicates per each treatment and five controls (PAALME, 1997).

In each hour the changes in the dissolved oxygen concentration in the bottles were measured by an oxygen meter OXI 92. Every second hour the water in the incubation bottles was changed. The incubation lasted 24 hours. Changes in oxygen were converted to the percentage of dry weight increment by standard methods (STRICKLAND, 1960) assuming a photosynthetic quotient of 1.2 for the expression of the rates of net photosynthesis.
Using similar methods the seasonal changes in the daily net production of *Furcellaria* and *Pilayella* were estimated at different depths in the coastal sea of Seili Island, SW Finland (60°14' N; 21°58' E) during 1996–97 (Paalme and Mäkinen, 1997). The studied two areas were similar in terms of salinity, temperature, nutrient concentrations and light regime. Based on Seili data, the relationships between depth and algal production were used for the budget calculations in Köiguste Bay.

**Grazing experiments.** Grazing experiments were performed in 5 litre glass jars. Adult *Idotea* were fed separately with *Furcellaria* and *Pilayella*. We added an average 15 specimens (0.2 g dw) of *Idotea* and 9.5 g ww (2.5 g dw) of *Furcellaria* or 1.3 g ww (0.1 g dw) of *Pilayella* to each jar. The control contained only algal material. Altogether 60 jars (15 replicates for each treatment and control) were deployed in the experiment. The jars were closed by a sieve of 0.2 mm mesh size to minimise the risk of migration but at the same time assure sufficient water exchange in the incubation jar. The incubations were performed at 0.5 m depth during 5 days in July and October 1998. The mesh was cleaned twice a day to avoid clogging by floating filamentous algae. Oxygen, salinity and temperature were regularly measured. Low oxygen concentrations were never observed. The survival rate of experimental animals was 100%.

The wet weight of algae was found prior and after the experiment to the nearest of 0.01 g. Before weighing the algae were gently dried with blotting paper until the paper did not become wet any more. In the laboratory the ratio of wet to dry weight (3 days at 60°C) was obtained for each season.

**Habitat preference.** The habitat preference of *Idotea* was investigated experimentally in July and October 1998. We placed 10 individuals of *Idotea* and small tufts of *Furcellaria* and *Pilayella* on 30 x 30 cm plastic trays filled with natural brackish water of 6 PSU. The coverage of *Furcellaria*, *Pilayella* and unvegetated area was 20, 20 and 60%, respectively. The temperature and light regime were similar to that of the ambient sea. Every second hour we estimated the number of *Idotea* on *Pilayella*, *Furcellaria* and the unvegetated area.

**Statistical analysis.** A significance level of 0.05 was adopted for all statistical tests. After testing for normality of the data (Kolmogorov–Smirnov test for goodness of fit) and homogeneity of variance (Bartlett’s test and Hartley’s test) analysis of variance (ANOVA) was performed on the daily net production of algae, idoteid grazing and habitat preference. In order to describe the relationship between depth and daily net production of algae the regression technique was used (Sokal and Rohlf, 1981).

### 3. RESULTS

*Fucus vesiculosus* and *Furcellaria lumbricalis* prevailed in the benthic vegetation of Köiguste Bay up to 1995 (Fig. 2). *Pilayella littoralis* dominated along most studied depth ranges in 1998. The species occurred as epiphytic or epilithic at lower depths and freefloating at higher depths. During the study period the average biomass of the most common herbivore, *Idotea baltica*, increased about hundred times. If *Idotea* previously inhabited *Fucus* bushes then nowadays the species is mainly found within the vegetation of *Furcellaria* and *Pilayella*. In 1998 we found a significant correlation between the biomass of *Idotea* and *Pilayella* ($r^2 = 0.98$, $p < 0.001$, $n = 12$) and between *Idotea* and *Furcellaria* ($r^2 = 0.10$, $p = 0.03$, $n = 12$).
Depth had no significant influence on the production of *Furcellaria* in July and October and on the production of *Pilayella* in July. Therefore, the net production measured at 0.5 m was extrapolated to the deeper areas in order to estimate the population growth increment of *Furcellaria* and *Pilayella* in Kõiguste Bay. The regression describing the relationships between depth \((D, \text{m})\) and daily net increment \((P, \% \text{ of } \text{dw } \text{d}^{-1})\) of *Pilayella* in October is as follows:

\[
P_{\text{October}} = -0.548 \times D + 5.234 \quad (r^2 = 0.79; \ p < 0.001).
\]

Average daily net production of *Furcellaria* was significantly higher in July than in October (one-way ANOVA \(p < 0.001, \ n = 10\)). On the contrary, *Pilayella* had a significantly higher production in October as compared to July (one-way ANOVA \(p < 0.048, \ n = 10\)). Maximum values of daily dry weight increment of *Furcellaria* and *Pilayella* were 1.1 and 5\%, respectively (Fig. 3).

*Idotea* grazed significantly more on *Pilayella* than *Furcellaria* both in July and October. However, the grazing values were strongly dependent on the season and the species considered (two-way ANOVA \(p_{\text{plant}} < 0.001, \ p_{\text{month}} < 0.001, \ p_{\text{plant}\times\text{month}} < 0.001, \ n = 60\)). The daily consumption of *Furcellaria* (mg dw *Furcellaria* per g dw *Idotea*) varied from 3 mg in October to 20 mg in July. The corresponding values for *Pilayella* were 27 and 49 mg.

Low algal production and high intensity of herbivory resulted in a relatively high grazing pressure (% of algal production grazed daily) on *Pilayella* in July (Figs. 3, 4). On the other hand, the grazing pressure on *Pilayella* was very low during October due to a high algal production and lower grazing values. The seasonal differences in the grazing pressure of *Furcellaria* by *Idotea* were not so strong as for *Pilayella* (two-way ANOVA \(p_{\text{plant}} = 0.074, \ p_{\text{month}} < 0.001, \ p_{\text{plant}\times\text{month}} < 0.001, \ n = 60\)). *Idotea* consumed up to 2.2\% of the net production of *Furcellaria* in July and 1.2\% in October. Same values for *Pilayella* were 4.7 and 0.7\% (Fig. 4).

Habitat choice experiments showed that *Idotea* preferred significantly *Furcellaria* to *Pilayella*. This difference was highest in October night and lowest in July night (three-way ANOVA \(p_{\text{species}} < 0.001, \ p_{\text{species}\times\text{month}} < 0.001, \ p_{\text{species}\times\text{month}\times\text{light}} = 0.022\), other terms were insignificant at \(p > 0.05, \ n = 204\)) (Fig. 5).

4. DISCUSSION

Invertebrate herbivory is considered as a major factor determining the structure and development of macroalgal assemblages (e.g. Paine, 1974; Lubchenco, 1978, 1982; Hawkins and Hartnoll, 1983; Salemaa, 1987; Malm, 1999). On the other hand, the abundance of herbivores is regulated by the competition for food and predation (Menge, 1976; Lubchenco and Menge, 1978; Edgar, 1983; Holmlund et al., 1990). Hence, the fluctuations in the abundance of herbivores have drastic repercussions on the dynamics of their competitors, predators and macroalgae (Barnes and Hughes, 1988).

In the Baltic Sea the most prevalent benthic invertebrate herbivore is the marine isopod *Idotea baltica* (Jansson, 1974; Salemaa, 1979, Jansson et al., 1982). The species plays an important role in the dynamics of *Fucus vesiculosus* and *F. serratus* L. (Salemaa, 1987; Malm, 1999). Under favourable conditions, such as an outbreak of
Pilayella littoralis, warm summer and diminished predation by fish, the density of Idotea may rapidly increase. Following overgrazing, in turn, leads to a serious decline or even disappearance of Fucus spp. in the area (Kangas et al., 1982; Malm, 1999). After eliminating Fucus the dense population of Idotea is expected either to crash down or switch into an alternative diet. The change in the diet may set the ecosystem even more out of balance as other macroalgal species have not adapted to the intensive herbivory by Idotea.

According to the literature idoteids are able to feed on green, red and brown algae and also vascular plants (Ravanko, 1969; Nicotri, 1980; Robertson and Mann, 1980). The food preferences may be determined either by the nutritional quality (Masterson, 1998), morphology (Hacker and Madin, 1991) or colour of algae (Salemaa, 1987).

During this investigation we observed major changes in the algae–herbivore relationship. After the outbreak of Pilayella the stands of Fucus have almost disappeared in Kõiguste Bay. At the same time the biomass of Idotea has explosively increased and its depth distribution has considerably widened. If Idotea previously inhabited the Fucus zone then nowadays it is found within the vegetation of Furcellaria and Pilayella.

The spatial distribution of Idotea followed that of Pilayella. The grazing pressure was higher on Pilayella than Furcellaria. On the other hand Idotea highly preferred Furcellaria as a habitat in the experimental conditions.

These results suggest that the habitat selection of Idotea is driven by both the food quality and the morphology of algae in Kõiguste Bay. It is very likely that Furcellaria offers a better refuge from predators whereas Pilayella serves as a better food. The maximum density of Idotea was observed in the shallower areas where the proportion of epiphytic Pilayella on Furcellaria was highest. Removing fast-growing epiphyte, Idotea also contributes to the persistence of slow-growing Furcellaria. The advantageous effect of herbivores on the growth of macroalgae has been previously documented (e.g. Brawley and Adey, 1981). By favouring the persistence of perennial macrophytes (Lubchenco, 1983) herbivores stabilise the benthic community and contribute to the maintenance of diversity.

We conclude that despite its occasional harmful effect on Fucus, Idotea is not able to regulate the biomass of Pilayella in Kõiguste Bay. On the other hand, it is likely that Idotea protects the algae that have strong thalli (e.g. Furcellaria) from excessive epigrowth by a “nuisance algae” Pilayella.

5. ACKNOWLEDGEMENTS

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Figure 1. Study area. The circle shows the location of Kõiguste Bay.
Figure 2. Average biomass distribution (g dw m\(^2\) ± SE) of dominant macroalgal and herbivore species in Kõiguste Bay during 1995 and 1998.
Figure 3. Average net production of *Furcellaria* and *Pilayella* and the corresponding  idoteid grazing expressed as the percentage of algal dry weight increment/decrement (± SE) in 24 hours.
Figure 4. Average percentage of algal daily net production consumed by *Idotea* (± SE).
Figure 5. Habitat choice of *Idotea* expressed as the average percentage of time spent (± SE) in different “biotopes”.
CONCEPTUALIZATION

The knowledge about the processes and factors that influence the distribution of natural resources and the role of competition and cooperation in shaping the outcomes is essential to understand the complex interactions within ecosystems. This chapter aims to explore the interplay between competition and cooperation, focusing on how these mechanisms contribute to the distribution of resources and the overall ecological balance.

The focus will be on a case study of an example ecosystem, where the dynamics of competition and cooperation are examined in detail. By analyzing the interactions and the resulting outcomes, we can gain insights into the principles that govern ecological systems.

To illustrate this, we will use the concept of a hypothetical ecosystem, which serves as a model to explore the underlying mechanisms. This ecosystem, though simplified, allows us to delve into the complexities of resource distribution and the role of competition and cooperation.

In the next section, we will present a detailed analysis of the ecosystem, highlighting the key factors that influence the distribution of resources and the dynamics of competition and cooperation. Through this analysis, we will uncover the underlying mechanisms that shape the ecological balance.

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Competition for food between the introduced polychaete *Marenzelleria viridis* and the resident amphipod *Monoporeia affinis* in the Baltic Sea (manuscript).
COMPETITION FOR FOOD BETWEEN THE INTRODUCED POLYCHAETE MARENZELLERIA VIRIDIS AND THE RESIDENT AMPHIPOD MONOPOREIA AFFinis IN THE BALTIC SEA

Jonne Kotta & Emil Ölfsson

Abstract. Interspecific competition for food between the introduced polychaete Marenzelleria viridis and the native amphipod Monoporeia affinis was studied in a laboratory experiment. Amphipods and polychaetes were kept in microcosms with sediment and continuous supply of cooled water for two months. M. viridis depressed the growth in adult amphipod length whereas juveniles were not affected. M. viridis had practically no influence on the mortality and weight increment of M. affinis. At higher amphipod densities M. viridis had no effect on M. affinis showing that intraspecific competition was stronger than interspecific competition. However, when food was not limiting the growth of M. affinis the values of juvenile length and weight were lower in the presence of M. viridis indicating also the interference competition between amphipods and polychaetes. The results of this experiment give support to the hypothesis that the decline of amphipod densities in the field is due to the competitive interactions between M. viridis and M. affinis.

Key words: Baltic, competition, laboratory experiment, Marenzelleria, Monoporeia

INTRODUCTION

The knowledge about the processes regulating animal populations is essential for understanding the dynamics of natural systems. Hence, the role of competition, predation and parasitism as regulatory or density-dependent processes has been the subject of many publications during recent years (e.g. Barnes & Hughes 1988, Begon et al. 1996).

The Baltic Sea is one of the world’s largest brackish waterbodies. Owing to low salinity, short developing time and isolation, only a few species have been able to adapt to the local conditions (Segerstråle 1957). Soft-bottom assemblages below the thermocline show particularly low diversity consisting, for example in the Baltic proper, of only a few of macrofauna and about 40 to 50 meiofauna species (Segerstråle 1957, Järvekülg 1979, Aarnio et al. 1991, Ölfsson & Elmgren 1997).

In this vast area the deposit feeding amphipod Monoporeia affinis (Lindström) may be ranked among most numerous invertebrates reaching densities up to 4000 ind m⁻² (Järvekülg 1973, 1979). In March–April when juveniles (0+) are released from the marsupium the natural abundance may even exceed 10,000 ind m⁻² (Järvekülg 1973, Sarvala & Uitto 1991). The amphipods may affect the structure of benthic assemblages through high consumption of sedimented phytoplankton (Uitto & Sarvala 1991, Lehtonen & Andersin 1998) and bioturbation (Elmgren et al. 1986, Ölfsson & Elmgren 1991, Ejdung & Elmgren 1998). The amphipods are predated by fish (Segerstråle 1937, Aneer 1975) and benthic invertebrates (Abrams et al. 1990, Hill et al. 1990, Hahtela

Levinton (1972) argued that deposit-feeders ought as a rule to be food limited and competition between them should be intense. There are several studies that indicate competition for food in soft bottom communities (Ólafsson & Persson 1986, Ólafsson & Moore 1990, Ólafsson et al. 1994). Is it likely that intra- or interspecific competition occurs in *M. affinis* populations in the Baltic Sea? Amphipods, both juveniles and adults, share same food resources, i.e. sedimented phytoplankton, and habitat with other deposit-feeding species. Oscillations in the numbers of *M. affinis* correlate with primary production values (Elmgren 1978, Uitto & Sarvala 1990, Sarvala & Uitto 1991) and the growth of amphipods seems to be density dependent (Sarvala 1986, Leonardsson 1994). Besides, there is some experimental evidence about intra- and interspecific competition for food between *M. affinis* and sibling species *Pontoporeia femorata* Kröyer (Hill & Elmgren 1987, Hill 1992). This suggests that the amphipod populations are normally food limited in the northern Baltic Sea (Elmgren 1978, Sarvala & Uitto 1991) and intraspecific competition is a likely explanation for annual fluctuations in the field (Sarvala 1986).

Since 1985 the detritus feeding polychaete *Marenzelleria viridis* (Verrill) has invaded large parts of the Baltic Sea (e.g. Essink & Kleef 1993, Kotta & Kotta 1998). In some areas it has become a dominant macrofauna species at densities up to 270,000 ind m\(^{-2}\) (Zettler et al. 1995). There exists circumstantial evidence that after the invasion of *M. viridis* the densities of the shallow water amphipod *Corophium volutator* (Pallas) (Atkins et al. 1987, Zettler 1996), the polychaete *Nereis diversicolor* (O. F. Müller) (Atkins et al. 1987, Essink & Kleef 1993) and the deep-water amphipod *M. affinis* have dropped considerably (Kube et al. 1997).

In this paper we discuss whether the introduced polychaete *M. viridis* has a negative effect on amphipod *M. affinis*. The main hypothesis are as follows:

1. The interspecific competition for food is likely between *M. viridis* and *M. affinis*.
2. The survivorship and growth rate of *M. affinis* are smaller in presence of *M. viridis*.
3. The effect of intra- and inter-specific density dependence is more pronounced at lower food concentrations and higher densities of *M. affinis*.

**MATERIAL AND METHODS**

Sampling of sediment and *Monoporeia affinis* was performed at a 28 m deep muddy station near the island of Askö, in the north-western Baltic Sea proper (58°49' N, 17°34' E). Prior to the onset of spring bloom (10 March 1999), sediment samples were taken with a van Veen bottom grab. This sediment was sieved through a 300 μm mesh and stored aerated at 7°C in the dark. *M. affinis* were collected with a benthic sledge (Blomqvist & Lundgren 1996) 4 days before the start of the experiments. The sediment was immediately sieved through 1 and 0.5 mm sieves and adults (1+) and juveniles of *M. affinis* (0+) were picked up in batches of 10 by means of a small piece of nylon.

*Marenzelleria viridis* were collected from the sandflat in Greifswalder Bodden, southern Baltic Sea (54°09' N, 13°38' E) on 16 April and held with sediment at 7°C. As
the salinity in Greifswalder Bodden and the Askö area was similar (−6 PSU) the polychaetes were not specially treated or acclimatised.

Two days before the start of the experiment the sediment was thoroughly mixed to ensure homogeneity. Microcosms, which consisted of plastic jars (100 cm³), were filled with a 6 cm layer of sediment and 6 cm layer of water and allowed to settle for 24 h (Fig. 1). Then polychaetes were randomly taken and added to the microcosms in the appropriate abundances for each treatment (Table 1). One day later (30 April) Monoporeia affinis were added. The microcosms were supplied with filtered (20 μm) seawater (temperature 6.6°C, salinity 6.0 PSU) at an average flow rate of around 25 ml min⁻¹.

The animals were fed over three weeks with a mixture of the diatoms Skeletonema costatum (Greville) Cleve (60%) and Nitzschia closterium (Ehrenberg) W. Smith (30%) and other algae (10%). The algae were cultured at 15°C in artificial seawater (Kester et al. 1967) at a salinity of 15 PSU with added nutrients, trace metals and vitamins (Guillard 1975). Prior to feeding the salinity of the culture was decreased down to 6–7 PSU. During feeding the water flow was stopped for 5 h. The feeding procedure was carried out until the amount of food reached the typical spring bloom sedimentation for the Askö area (5–8 g C m⁻²).

The experiment was run for 64 days. Animals were sieved out using a 300 μm net and preserved in a 4% formaldehyde solution. From each microcosm, all animals were counted and the length and dry weight (60°C, 48 h) of 20 randomly chosen individuals were measured. The length was measured with the aid of camera lucida using a light microscope.

Three-way analysis of variance was performed to test the effects of amphipod density, feeding and the presence of M. viridis on the survival, weight and length of M. affinis. Prior to the analysis, Bartlett’s test was used to check the assumption of homoscedasticity (Sokal & Rohlf 1981).

**RESULTS**

The presence of M. viridis, density of amphipods and feeding did not affect the survival of M. affinis (Table 2, Fig. 2). When no food was added adult survival gradually decreased (no significant difference) with increasing number of amphipods. Juvenile survival had greater variation between treatments than adult survival. In the presence of M. viridis and when amphipods were fed, juvenile survival was significantly lower at densities of 40 than at densities of 20. Other differences were not significant. Similarly, the survival of M. viridis was independent of the age or density of amphipods and feeding (Table 2, Fig. 3).

Amphipod density and feeding contributed to the variance of mean dry weight of both juvenile and adult M. affinis. The effect of the presence of M. viridis was not significant (Table 2, Fig. 4). Amphipod weights were higher when they were fed. The weight of adults decreased with increasing amphipod density in the treatments where M. viridis were not added. In the presence of M. viridis the weight was independent of the amphipod density. At densities of 20 the weight of amphipods was lower with M. viridis than in treatments with amphipods only. The weight of juveniles decreased with increasing amphipod density only when amphipods were fed. The effect of
\textit{M. viridis} on the weight of juveniles was contradictory being either positive (no feeding) or negative (feeding).

\textit{M. viridis} and feeding had significant effect on the mean length of adult amphipods whereas amphipod density and feeding had an effect on juveniles, correspondingly (Table 2, Fig. 5). When food was added amphipods grew bigger. \textit{M. viridis} resulted in lower length of adult amphipods. Adult length was significantly higher at densities of 20 amphipods than at other densities in treatments where animals were fed and \textit{M. viridis} were not added. Juvenile length decreased with amphipod density in treatments where food was not added. When feeding no density dependence was observed indicating that food was not limiting the growth of juvenile amphipods in these treatments.

\section*{DISCUSSION}

\textit{M. viridis} had a clear negative effect on adult \textit{M. affinis} in terms of amphipod growth in length. Comparable adverse influence on the weight was seen only for adults at a density of 20 amphipods, i.e. 2000 ind m\textsuperscript{-2}. Such density is equivalent to the natural densities normally found in the study area (Cederwall 1977). Earlier field observations have shown that the adults of \textit{M. affinis} lose weight immediately after the spring bloom (Cederwall 1977). This may explain the poorer performance of weight over the length of \textit{M. affinis} in discriminating inter- and intra-specific competition.

At higher amphipod densities the effect of \textit{M. viridis} was not statistically significant indicating that intraspecific competition was the main regulatory process in these treatments. Similarly to Hill (1992) amphipod weight and length were significantly greater at lower densities. However, when amphipods were fed (equivalent to spring bloom), the variation in juvenile length and weight was independent of the amphipod density and these values were always lower in the presence of \textit{M. viridis}, indicating interference competition between polychaetes and amphipods.

Amphipod mortality was not increased by their increasing density nor was it affected by the presence of \textit{M. viridis}. Instead, lower food concentration resulted in greater juvenile mortality. The results of the present experiment suggest that the availability of food sets the limits to the amphipod density and the occurrence of interference competition between the amphipods is less likely. This is in contradiction to the results of Hill (1992), who found that juvenile mortality is mainly induced by higher amphipod densities.

The evidence for direct intra- and interspecific competition is often circumstantial; nevertheless, Levinton (1979) argued that it must occur. One might expect that interactions would be most intense within feeding types rather than between completely different general types.

Since the invasion of polychaete \textit{M. viridis}, the density of several common deposit feeders has declined in the Baltic Sea (e.g. Essink & Kleef 1993, Zettler 1996). This has been attributed to the competitive interactions between the introduced polychaete and native fauna. All the evidence we have on the influence of this polychaete on other species both in the Baltic and elsewhere, are however circumstantial. This is the first manipulative experimental study demonstrating the negative effect of \textit{M. viridis} on the amphipod \textit{M. affinis}. The polychaetes depressed the growth in amphipod length and to
some extent in weight but did not affect its survival. The results indicated that the suppression was due to competitive interactions for food. However, the effect was not so strong as we assumed.

Competitive interactions for food between *M. viridis* and *M. affinis* may be severer in the field than shown in our experiments. There are three major reasons for this. (1) We used low densities of polychaetes, i.e. 200 ind m⁻², whereas the abundances recorded in the Baltic may be as high as 270,000 ind m⁻² with an average at 500–1000 ind m⁻² (Zettler 1997). (2) Besides, the experimental animals were small, though typical for the north-eastern Baltic Sea. (3) Being collected from the shallow and organically enriched area, it is likely that the polychaetes were not fully adapted to cold and oligotrophic conditions.

Thus, the reduction in the growth of amphipods due to the competitive interactions between *M. viridis* and *M. affinis* is expected to have an effect on the duration of amphipod life cycle, i.e. recruitment is prolonged and fecundity is reduced. Consequently, amphipods are longer exposed to possible predation and, hence, their population size is likely to be diminished. We expect that the negative effect of *M. viridis* on the population of *M. affinis* will have drastic repercussions on higher trophic levels such as intermediate predators (Haaitela 1990, Hill & Elmgren 1992, Ejdung 1998) and fish species (Aneer 1975, Aarnio et al. 1996) that rely on benthic fauna as food resource. The overall community structure is also likely to change with some species gaining from bioturbating activities of the polychaete while others may reduce in abundance or disappear.

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Table 1. Experimental setup of investigating the effect of *Marenzelleria viridis* on juvenile and adult *Monoporeia affinis* at different population densities and feeding regimes.

<table>
<thead>
<tr>
<th>Treatment</th>
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Table 2. Three-factor ANOVA of effects of the presence of *Marenzelleria viridis* (0, 2 individuals), amphipod density (20, 40, 80 individuals), and addition of food (feeding, no feeding) on survival, length and weight of juvenile and adult *Monoporeia affinis* and the effects of amphipod density (20, 40, 80 individuals), age (0+, 1+) and addition of food (feeding, no feeding) on the survival of *M. viridis*. Interactions of different terms were not statistically significant (*p*>0.05).

<table>
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<th>P</th>
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<tr>
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<tr>
<td>B: Density</td>
<td>2</td>
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</tr>
<tr>
<td>C: Food</td>
<td>1</td>
<td>1.41</td>
<td>ns</td>
</tr>
<tr>
<td>WEIGHT</td>
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<td></td>
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<td>A: <em>Marenzelleria</em></td>
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<td><strong>Monoporeia adults</strong></td>
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<td>WEIGHT</td>
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<td>3.43</td>
<td>0.040</td>
</tr>
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<tr>
<td>LENGTH</td>
<td></td>
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</tr>
<tr>
<td>A: <em>Marenzelleria</em></td>
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<td>3.41</td>
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<tr>
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<tr>
<td>C: Food</td>
<td></td>
<td></td>
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</tbody>
</table>

*ns* is equivalent to *p*>0.05
Figure 1. Experimental setup.
Figure 2. Survival of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*.
Figure 3. Survival of *M. viridis* in relation to feeding, amphipod age (juv – juveniles, ad – adults) and density.
Figure 4. Weight of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*. 

---

**Adults & Feeding**

- **Density of *M. affinis*, ind:**
  - 20
  - 40
  - 80

**Juveniles & Feeding**

- **Density of *M. affinis*, ind:**
  - 20
  - 40
  - 80

---

**Adults & no feeding**

- **Density of *M. affinis*, ind:**
  - 20
  - 40
  - 80

**Juveniles & no feeding**

- **Density of *M. affinis*, ind:**
  - 20
  - 40
  - 80
Figure 5. Length of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*. 
EFFECT OF DISPOSE AND ENERGY SUPPLY ON THE LOW INCOME HAMLETT COMMUNITY IN THE NEW JERSEY PAINTED

Chapter III

In this chapter it is desirable to determine the conditions of low energy consumption in the low income housing stock. The analysis of energy consumption in low income housing will be attempted first to determine the extent of energy consumption in low income housing, and second to determine the effectiveness of energy conservation measures. The analysis will be based on the data from the Energy Consumption Survey of the New Jersey Department of Energy. The survey was conducted in 1970 and the results were published in 1971.

5. INTRODUCTION

Physical comfort of the occupants is a key factor in providing a comfortable living environment. Inadequate comfort can lead to health problems, reduced productivity, and increased energy consumption. This chapter aims to analyze the energy consumption patterns in low income housing and identify potential strategies for reducing energy usage. The analysis will be conducted through a comprehensive review of existing literature and a statistical analysis of data from the Energy Consumption Survey of New Jersey.

The chapter will be divided into three sections: an overview of the energy consumption in low income housing, an analysis of energy conservation measures, and a discussion on the implications of the findings. The chapter concludes with a recommendation for further research and policy implications.
EFFECT OF DIFFUSE AND POINT SOURCE NUTRIENT SUPPLY ON THE LOW DIVERSE MACROZOOBENTHIC COMMUNITIES OF THE NORTHERN BALTIC SEA

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2Institute of Zoology and Hydrobiology, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia
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Short title: Effect of diffuse and point source nutrient

ABSTRACT

Soft bottom macrozoobenthic communities from the coastal sea area of Helsinki (south Finland) and Saaremaa Island (west Estonia) were compared in order to evaluate the effects of diffuse and point source nutrient supply. The coastal sea area of Helsinki receives a moderate load of municipal sewage water and the latter is ranked among the most undisturbed ecosystems in the northern Baltic Sea. The species composition and dominance structure were similar in both the studied areas indicating that different sources of eutrophication (i.e. local or basin wide) have similar consequences for the macrozoobenthic communities. However, functional diversity was higher in the Saaremaa area as the higher share of herbivores and suspension feeders were found in the area.

Keywords: Baltic Sea, eutrophication, macrozoobenthos, soft bottom

1. INTRODUCTION

Increasing rate of urbanisation results in a higher load of nutrients into adjacent water-bodies. Consequently, phytoplankton blooms and a decrease of light attenuation are expected (Launiainen et al. 1989, Nixon 1995). Poor light conditions restrict macroalgal communities to shallower areas (Kautsky et al. 1986) creating a severe stress for the benthic fauna relying on a macroalgal belt for shelter, food or reproduction (e.g. Kautsky et al. 1992). On the other hand, high phytoplankton biomass supports abundant but low diverse filter- and detritus feeding communities. Further input of nutrients may lead to oxygen deficiency which results in extensive mortality of benthic animals or even disappearance of entire macrobenthic communities (Larsson et al. 1985, Josefson and Widbom 1988, Rosenberg and Loo 1988, Bonsdorff et al. 1997, Kotta and Kotta 1997).

Numerous papers have been written about the effects of increased nutrient supply on benthic communities (e.g. Cederwall and Elmgren 1980, Andersin 1986, Brey 1986, Elmgren 1989, Bonsdorff et al. 1991, Warwick and Clarke 1991, Zmudzinski and Osowiecki 1991). Benthos studies have led to the development of the concept of
indicator species and communities of different trophic zones (Leppäkoski 1975, Pearson and Rosenberg 1978, Järvekülg 1979). It is summarised that increasing eutrophication leads to an increased biomass of macrozoobenthos above the halocline or a defaunation due to hypoxic or anoxic conditions in deeper waters (Laine et al. 1997, Modig and Ölafsson 1998).

Little is known about eutrophication processes in almost unstressed sea areas (e.g. Bonsdorff et al. 1997). In these areas the local input of nutrients are considered negligible and the dynamics of the system is mainly driven by the basin-wide processes such as the development of halocline causing long periods of oxygen deficiency (Andersin and Sandler 1991, Laine et al. 1997). In the shallower areas of the Baltic the species diversity has remained very high (Bonsdorff et al. 1997, Kautsky et al. 1999). Similarly to more eutrophied areas, however, the community composition has changed and the number of species has diminished during last decades (Kotta and Kotta 1997).

In this study we compare the output of diffuse and point source nutrient supply by estimating the structure of benthic communities. The aim of the paper is to analyse whether different sources of eutrophication (i.e. local or basin-wide) lead to different ecological consequences. Due to the relatively stationary life, longevity and broad distribution macrozoobenthos reflects the organic enrichment of the sediment and, hence, is an important tool for the assessment of the state of the marine environment.

2. MATERIAL AND METHODS

2.1. Study area

Macrozoobenthos was sampled in two adjacent sea areas of Helsinki, the capital city of Finland (Fig. 1). Samples were collected from soft sediment between a depth of 0.5 and 10 m (Table 1). During sampling the presence of phytobenthos was estimated either visually or using a bottom scraper. The region is highly populated (2920 inhabitants per km²) and influenced by the moderate input of municipal wastewater. Daily load of nutrients is in order of magnitude of 0.15 t for phosphorus and 7.5 t for nitrogen (Pesonen et al. 1994).

The Seurasaari Bay is situated in the suburban area of Helsinki. It is a wide, shallow area with a narrow and 6–10 m deep strait connecting the bay with the open sea. Prevalent bottom types are silty and silty clay sediments with a small gravel fraction. Average depth of the bay is 2 m. Due to the isolation, Seurasaari is seemingly the most eutrophied among the studied areas.

The Vuosaari sea area is situated about 10 km eastwards from Seurasaari. It is characterised as a relatively open sea-area with few scattered islands. Approximately 1/6 of the nitrogen and phosphorus load from Helsinki is discharged in the vicinity of Vuosaari. There is a strong correlation between depth and the type of substrate as stone bottoms are predominant at the sea level and replaced by gravel bottoms at 1–2 m and by silty or silty clay sediments at 2–2.5 m.

In the isolated and open sea areas of Saaremaa Island (Fig. 1) samples were taken between a depth of 0.5 and 6 m (Table 1). The coastal sea of the island is characterised as a relatively unstressed environment. The urbanisation level of the Saaremaa Island is one of the lowest in Estonia (14 inhabitants per km²) and less than 7 % of the land is
cultivated. The load of nutrients may be considered negligible in the coastal sea of Saaremaa. The region is supplied by diffused nutrients from the open part of the Gulf of Riga. However, the gulf as a whole is a relatively eutrophic system with its annual primary production being almost twice as high as in the Baltic Proper (Yurkovskis et al. 1993, Mägi and Lips 1998).

Because of comparable soft-bottom macrozoobenthic communities, the coastal sea of Saaremaa is well suited as a reference area to Seurasaari and Vuosaari. Similarly to the Helsinki areas Saaremaa Island has a diverse coastline with more than 600 islets (Ratas and Nilson 1997). Salinity varies around 5–6 PSU in both areas and no oxygen deficiency was recorded in the study areas.

Benthic samples were collected using a modified Petersen bottom grab (0.017 m²) in the coastal sea of Saaremaa in 1993 and in Seurasaari in 1995. An Ekman-Lenz bottom sampler (0.04 m²) was used in Vuosaari in 1996. Sampling was performed during late summer. At each site one sample was taken (Table 1).

Sediments were washed through a nylon net bag of 0.25 mm mesh size and the samples were preserved in 4% buffered formaldehyde solution. In the laboratory, the samples were sorted under a stereo dissecting microscope. Total wet weight for each taxon was weighed to the nearest 0.5 mg.

2.2. Statistical analysis

A significance level of 0.05 was adopted to all statistical tests. After testing for normality of the data (Kolmogorov-Smirnov test for goodness and fit) and homogeneity of variance (Bartlett’s, Hartley’s tests), two-way analysis of variance (Sokal and Rohlf 1981) of the effects of region and isolation was performed on the abundance and biomass of macrozoobenthos. The comparative plots of the relative proportions of biomass and abundance of each species in the community (k-dominance curves) were drawn. This method has been previously suggested to detect pollution effects on marine macrobenthic communities (Warwick 1986, Warwick et al. 1987). The abundance diversity is higher than biomass diversity under stable unpolluted conditions and vice versa in grossly polluted communities.

Additionally the non-metric multidimensional scaling analysis (Clarke and Warwick 1994) was run to see whether or not there were regional differences in the structure of invertebrate communities, and to evaluate which environmental factor might be responsible for these differences. An untransformed data of abundance and biomass of macrozoobenthic species was used to calculate the difference between the stations. Bray-Curtis similarity measure was used to construct the similarity matrices (Bray and Curtis 1957).

3. RESULTS

The two-way analysis of variance showed that isolation and region are important in explaining the variance of total macrozoobenthos abundance but only regional differences were significant for its total biomass (Table 2). The mean abundances were higher in Saaremaa than in Helsinki, and higher in isolated areas than in open areas.
(308 ind m⁻² in Vuosaari, 1620 ind m⁻² in Seurasaari, 1711 ind m⁻² in Saaremaa open sea areas and 1735 ind m⁻² in Saaremaa isolated sea areas). The mean biomasses were higher in Saaremaa (99 g m⁻²) than in Helsinki (31 g m⁻²). The differences were mainly attributed to the higher density of phytophilous gastropods (e.g. *Theodoxus fluviatilis* and *Bithynia tentaculata*) in the Saaremaa area. Polychaetes and oligochaetes were more abundant in the coastal sea of Helsinki. Isolation rank and area did not contribute to the variance of the biomass of Annelida, Crustacea, Insecta and Mollusca.

The share of four different trophic groups (herbivores, filter-feeders, omnivores and deposit-feeders) in the benthic community was calculated according to Järvekülg (1979). Deposit feeders dominated in the studied areas, especially in the coastal sea of Helsinki (Fig. 2). However, the areas were functionally different. The coastal sea of Saaremaa had higher proportion of herbivores as compared to Vuosaari and Seurasaari implying abundant macrovegetation in the region. Suspension feeders comprised about 50% of the total biomass in the open areas of Saaremaa Island being negligible in the other studied areas.

K-dominance curves depict the effect of environmental disturbance (including pollution and eutrophication) on the macrozoobenthos at different studied areas (Fig. 3). The communities of the coastal sea of Helsinki (Vuosaari and Seurasaari) and open areas of Saaremaa Island conform to the model of unpolluted type i.e. the biomass curve is above the abundance curve throughout its entire length. The isolated parts of the coastal sea of Saaremaa represent moderately polluted area.

Taking into account the abundance and biomass, we computed the aggregation pattern of sites with the multidimensional scaling analysis. It showed that the benthic communities of the coastal sea of Helsinki are more uniform than those of Saaremaa Island (Fig. 4). Isolation rank and the presence of macrovegetation contributed most to the variability of macrobenthic communities. The x-axis of the figure corresponds to the isolation rank of an habitat. Higher values matched to the open areas and lower values to the isolated areas. Insect larvae, Chironomidae, gastropods such as *Bithynia tentaculata* and partly *Theodoxus fluviatilis*, numerically dominated in the isolated sea areas. The characteristic species of the open sea were the bivalves *Macoma balthica*, *Mya arenaria*, *Mytilus edulis*, and crustaceans *Idothea balthica*, *I. viridis*, *Gammarus salinus* and *G. oceanicus*.

The y-axis shows the presence of macrovegetation. The lowest values refer to areas without vegetation, the higher values to the communities rich in attached macroalgae such as *Potamogeton pectinatus*, *P. perfoliatus*, *Ruppia maritima* and *Zannichellia palustris*. Rich benthic vegetation supports higher densities of gastropods, hence, the y-axis mainly reflects the changes in the proportion of *B. tentaculata* and *T. fluviatilis* in the community. The factor contributing to the variance along the y-axis of the analysis of biomass structure is less clear.

4. DISCUSSION

In this study we compared the soft bottom invertebrate communities at areas subjected to diffused (Saaremaa) and point source nutrient input (Helsinki). The coastal sea of Saaremaa had higher trophic diversity than the sea areas adjacent to Helsinki. Macrobenthic communities were dominated only by deposit-feeders in the coastal
sea of Helsinki. Besides deposit-feeders, a significant proportion of filter-feeders and herbivores were found in the coastal sea of Saaremaa. The higher niche diversity is probably due to the presence of benthic vegetation offering feeding grounds for herbivores and secondary substrate for suspension feeders. Macrophyte beds are known to have a higher abundance of epibenthos and infauna than comparable unvegetated bottoms. This has been attributed to the higher sediment stability, habitat complexity, more diverse food resources and lower predation pressure (Welsh 1980, Barnes and Hughes 1988, Wilson et al. 1990).

On the other hand, the k-dominance curves indicated that the environmental disturbance is highest at the isolated areas of the Saaremaa study area. The latter is classified among the most conserved ecosystems in Estonia. However, it may receive nutrients from the Gulf of Riga. Shallow depths and isolation favour light penetration and nutrient accumulation and, therefore, we may expect a higher productivity and a fast eutrophication processes even there.

Multidimensional scaling analysis is considered more sensitive than species independent methods (e.g. ANOVA or similarity indices) in discriminating between sites or times (Warwick and Clarke 1991). The communities of the coastal sea of Saaremaa and Helsinki do not form two distinguished statistical groups as expected from the differences in their urbanisation level. In general, the communities were very homogeneous. *Macoma balthica* was the most common species in the whole study area. Both areas were characterised by relatively high occurrence of insect larvae (mostly *Chironomidae*), oligochaetes and polychaetes. Abundance and biomass values of crustacean were low. Similarly to previous statistical analysis MDS analysis stressed higher benthic diversity in Saaremaa i.e. higher dissimilarities between stations.

It is known that abundance of benthic invertebrates increases with the organic content of the sediment (i.e. eutrophication level) (Bonsdorff et al. 1997). We found no evidence of a higher total abundance in presumably more polluted environments. On the contrary, abundances were higher in the coastal sea of Saaremaa in 1990s. Hence, we may say that eutrophication has little effect on the community structure of benthic fauna in silty or clay bottom biotope.

As a conclusion, the structure of zoobenthos communities of the Saaremaa and Helsinki areas are alike. It suggests that both communities are affected by similar disturbance. That is different sources of eutrophication (local vs basin-wide) results in the similar consequences on soft sediment in terms of macrozoobenthos. However, the zoobenthos of the coastal sea of Saaremaa Island is more diverse which refers to its higher functional diversity.

ACKNOWLEDGEMENTS

Authors are grateful to Mrs Tiia Rosenberg. This study was funded by Helsinki City Centre of Environment and Estonian Governmental Programmes no. 0200792s98 and 0200797s98.
REFERENCES


Table 1. Description of benthos samples: No = number of stations, depth = average sampling depth (with maximum and minimum values), sediment = percentage of clay, silt and mixed bottoms in the region.

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<tr>
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<td>30.8</td>
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<tr>
<td>Saaremaa open</td>
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<td>37.5</td>
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<tr>
<td>Vuosaari open</td>
<td>10</td>
<td>5.30 (3–10)</td>
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Table 2. Probability intervals of two-way analysis of variance (α = 0.05) for the abundances and biomasses of macrozoobenthos against isolation rank (open, isolated) and region (Saaremaa, Helsinki).

<table>
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<td>Vermes</td>
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<td>Crustacea</td>
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<td>Insecta</td>
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<td></td>
<td>Mollusca</td>
<td>0.458</td>
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</tr>
<tr>
<td></td>
<td>total</td>
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<td>0.013</td>
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<td>Abundance</td>
<td>Vermes</td>
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<td>Insecta</td>
<td>0.054</td>
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<tr>
<td></td>
<td>Mollusca</td>
<td>0.709</td>
<td>0.000</td>
</tr>
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</table>
Figure 1. Study area. Stars represent the location of the sampling stations. Seurasaari sea area, Arju, Kasti, innermost parts of Tepu and Kõiguste bays constitute isolated group and Vuosaari, Kuressaare, Sepamaa and open parts of Kõiguste and Tepu bays open sea areas, respectively.
Figure 2. Share of different trophic groups within zoobenthic communities in the coastal sea of Helsinki and Saaremaa.
Figure 3. K-dominance curves of biomass and abundance of zoobenthic communities in the study area.
Figure 4. Multidimensional scaling analysis by sites on the abundances and biomasses of zoobenthos in the coastal sea of Helsinki and Saaremaa.
Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s

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Shifts in the Gulf of Riga ecosystem in the period 1970-1990 are interpreted as a response of the biota to major deviations in climate and important changes in anthropogenic impact. The increase in eutrophication until the late 1980s, the long stagnation period of the deepwater layer in the Baltic Sea from the late 1970s to the early 1990s, and an increase in freshwater run-off favoured organisms preferring lower salinity and tolerating a higher eutrophication level. Simultaneously, the presence of cod in 1977-1985 may have contributed to a decrease in some marine demersal fish stocks. For the cold-water species, which are considered glacial relicts, the situation was worsened by warm winters during 1988-1993 favouring warm-water fauna. The decrease of freshwater run-off and anthropogenic pollution in the 1990s and the increase in water salinity and severity of winters have triggered opposite changes in the biota: the abundance of some previously depleted demersal fish species is increasing and feeding conditions of herring have improved. Furthermore, the non-indigenous species Cercopagis pengoi and Marenzelleria viridis appear to play an important role in the ecosystem of the Gulf of Riga in the 1990s.

Introduction

The Gulf of Riga is one of the most highly eutrophied areas in the Baltic (HELCOM, 1996). It supports a high fish production and presently accounts for about 4% of total fish landings in the Baltic Sea. Research of the ecosystem dates back to the early 1920s, with regular Estonian cruises starting in 1923 to measure abiotic and biotic parameters such as temperature, salinity, density, oxygen concentration, chlorine content, transparency, and water colour. Annual studies of the main commercial fish species and fish larvae started in 1946, of zooplankton in 1956, and of nektobenthos in 1974. Fish catches have been recorded since the turn of the century, but regular studies of the fish fauna were only begun in 1974. These investigations were accompanied by the recording of key abiotic parameters of the ecosystem. Most of this research has been dedicated to developing a better understanding of the factors influencing the dynamics of commercial fish stocks (Rannak, 1970; Erm, 1967; Kornilovs, 1993; Gaumiga et al., 1997).

Materials and methods

Mean water temperatures during summer (measured at 1 m depth in Pärnu Bay, June–August) and winter air temperatures (measured in Pärnu, December–March) and run-off from the Pärnu river (January–December) were calculated on the basis of daily measurements. Annual salinity means were computed from daily measurements at the surface off Kihnu Island during June–December (data from the Estonian Hydrometeorological Institute). In 1994–1997, bottom salinity
was determined from samples taken monthly at nine stations on the transect Pärnu Bay–Ruhnu Deep (Fig. 1) during experimental bottom trawl surveys. These monthly surveys were conducted on a small stern trawler (length 12.5 m, 90 HP) from April to November–December in 1974–1986 and 1994–1996, except in 1981–1986 when only between one and three surveys per year were carried out (in the autumn). The trawl hauls were made at 6, 8, 12, 15, 20, 25, 30, 35, 40 and 50 m depth during daylight. Mean trawling speed was 2.5 knots and haul duration was 30 min. Estimated trawl opening area was 40 m² and mesh size in the codend 8 mm (May–July 1994: 20 mm). Abundance of all species was determined by sorting the total catch or a suitable subsample. Because identification of Gasterosteus aculeatus and Pungitius pungitius may have been inaccurate during the first period, sticklebacks were not analysed at species level. Gobies (Pomatoschistus spp.) were not identified to species. Distribution of the seven most abundant fish taxa over the area was analysed using mean abundance values by depth strata. To account for the different depth coverage between periods, some adjustments to the original survey data were inevitable. For the shallower part, hauls at 5 m, 7 m, and 10–11 m depth in 1974–1986 were treated as replicates for the stations at 6 m, 8 m, and 12 m, respectively. Stations deeper than 40 m during 1994–1996 were interpreted as replicates of the 40 m station. To overcome the problem of unequal numbers of surveys over the years, catch per effort data were analysed using the GLM model:

$log (mean \ catch + 1) = year + month + e, \ \ (1)$

where mean catch is the monthly average catch by number of a species per 30 min haul. Year and month represent the year effect and month effect, and e is the error term.

The year effect was used as an index describing the dynamics of fish stock abundance. Index values were calculated for the seven most important marine fish species and glacial relics (the species having yielded a total catch of >500 individuals over all years). Dynamics in the abundance of less numerous species were estimated by comparing average values for the two periods (1974–1986 and 1994–1996) with the total. Since 1994, samples for estimation of the abundance and biomass of mesozooplankton, the food resources for pelagic and juvenile fish, were also taken during the surveys. Zooplankton was sampled at each station by vertical tows from bottom to surface with a large Juday net (mouth diameter 37 cm, mesh size 90 μm). Samples

Figure 1. Location of sampling stations in the Gulf of Riga along the transect fished during experimental bottom-trawl surveys from Pärnu Bay to Ruhnu Deep. Crosses denote single sites and short solid lines indicate transects for zoobenthos sampling. Filled circle shows sampling location of Neomysis integer. Additional sampling locations for Cercopagis pengoi are given by asterisks.
were preserved in 4% formaldehyde solution and analysed using routine methods. Annual means (± s.e.) of abundance and biomass of total zooplankton and copepods only were calculated on the basis of seasonal averages for the period 1994–1998.

The most abundant pelagic fish species (herring, *Clupea harengus membras* L., and sticklebacks) were selected for estimating feeding activity. For this purpose, the share of fish with empty stomachs was determined. Samples were collected from experimental trawl catches during day-time. Each sample generally consisted of 20 individuals. In total, 2570 herrings and 1130 sticklebacks were analysed. To balance different numbers of samples, annual means of the indices were calculated on the basis of monthly means during the main feeding period (adult herring: May–September; 0-group herring: August–November; sticklebacks: May–August).

Samples of the mysid *Neomysis integer* (Leach) were collected weekly during 1974–1996 by means of a Rass trawl (mesh size 0.4 mm; towing time 5 min; towing speed 1 km/h; filtrated water volume 17 ± 3 m³) at a fixed station (depth 10 m) in the north-east part of the Gulf of Riga (Fig. 1). This mysid migrates through this area toward the wintering areas in deeper parts of the basin during late summer and autumn. Annual relative abundance was calculated for the main migration period, September–October.

*Marenzelleria viridis* (Verrill) was studied in macrozoobenthos samples taken from 6 single stations and 10 transects from 0.1 to 15 m depth (Fig. 1) in July–August, 1994–1995. Below 15 m, samples were collected by Tvärminne sampler (0.03 m²), whereas a van Veen bottom grab (0.10 m²) was used in deeper parts of the basin. Transects consisted of 4–5 stations. Three replicate samples were taken at both single stations and along transects, and a total of 172 samples were analysed. Samples were sieved through 0.25 mm nylon mesh and biomass was calculated in dry weight.

**Results**

Freshwater input has generally increased during 1970–1990, followed by decline (Fig. 2a). A certain periodicity in summer water and winter air temperatures is also evident. Winters were generally colder in the second half of the 1970s and mid-1980s, and warmer during the first half of the 1970s and early 1980s. After a long period of warm winters during the late 1980s and early 1990s, mean winter air temperature shows a declining tendency since 1992, although winters still remained relatively warm. In contrast, summer water temperatures indicate a recent increase since 1993, the coldest summer on record (Fig. 2b). Salinity off Kihnu Island fluctuated around 6 during the 1970s but exhibited a decrease during 1979–1985 and reached the lowest level in the last year of the observations (Fig. 2c). Recent measurements in 1994–1997 suggest an increasing tendency in mean annual bottom salinity along the transect Pärnu Bay–Ruhnu Deep (variability range 4.75–5.66), annual averages remaining generally below yearly surface salinity off Kihnu Island in 1970–1989.

Abundance and biomass of total zooplankton and copepods show a general increase during 1994–1998. The two indices for copepods increased almost continuously from 20 to 51 m⁻³ and from 150 to 458 mg m⁻³, respectively. Abundance and biomass of the total mesozooplankton increased from 48 in 1996 to 143 m⁻³ and from 299 in 1995 to 809 mg m⁻³, respectively (Fig. 3). The increase was also evident in each of the two subareas identified (coastal region up to 15 m depth and the open part of the gulf) and by season.
However, the increase in mesozooplankton was more pronounced in open parts of the basin.

The cladoceran *Cercopagis pengoi* (Ostroumov), a recent invader of the ecosystem, was found, with a single exception, in all locations sampled in the northern and central parts of the basin (Fig. 4). Abundance was higher during a warm season in the shallow and sheltered Pärnu Bay (up to 800 m$^{-3}$) than in the middle of the Gulf of Riga (at 20–50 m, usually <40 m$^{-3}$) or in the western part of the basin (±10 m$^{-3}$). Another newcomer, the euryhaline polychaete *Marenzelleria viridis*, appeared in macrozoobenthos samples in the Pärnu Bay area and along the Saaremaa coast in 1994, although the species has been present in other parts of the basin since 1991. *M. viridis* constituted up to 6.9% of the total biomass of macrozoobenthos in several areas of the gulf, but its share remained below 1% in 59% of the samples (Fig. 4).

Stock abundance of *N. integer* has been significantly higher since 1988 than in previous years (Mann-Whitney U-test, p<0.01). Elevated abundance values have also been observed in 1981–1982 (Fig. 5). A significant positive correlation was found between the abundance and winter air temperature ($R=0.45$, p<0.05), indicating that a more abundant stock of this warm-water mysid develops after mild winters and *vice versa*.

The relatively high abundance of marine pelagic species (herring, sprat) and of cold-water, marine demersal species (smelt, eelpout, cod, gobies) in the 1970s has been followed by a marked decline in the 1980s. Recently, the stock condition of clupeoids has improved considerably. Smelt, eelpout, and gobies have
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Figure 6. Dynamics of the abundance-based year effect for selected fish in the Gulf of Riga over the years 1974-1986 and 1994-1996. Bars indicate the least significant difference for each entire time series (2* s.e.).

shown a more moderate increase in numbers and cod has been largely exterminated from the Gulf of Riga. In general, the year effect of sticklebacks exhibited, with deviations, an increasing tendency (Fig. 6). Of the less abundant fish species, only single specimens of sea snail Liparis liparis Ekström, sea scorpion Cottus scorpius L., and lumpsucker Cyclopterus lumpus L. were caught during 1994-1996 (means for 1974-1980: <0.4 individuals per survey) and four-horned sculpin Triglopsis quadricornis L. was not recorded (mean for 1974-1980: 0.2).

The percentage of empty stomachs, as an indicator of feeding activity (Fig. 7), displayed a generally decreasing tendency for adult herring in 1995–1998 (from 49% to 24%) and a more pronounced decline for 0-group herring (from 20% in 1994 to 6% in 1998). The share of sticklebacks with empty stomachs decreased only slightly during 1994–1997, but dropped considerably afterwards. Overall, feeding activity of plankton-eating fish appears to have increased over the recent 5-year period.

Discussion

Total zooplankton and copepods appear to have increased in the north-eastern part during recent years (1994–1998). From previous studies it is known that temperature regime and also eutrophication influence both species composition and abundance of zooplankton in the Gulf of Riga (e.g., Simm, 1982; Sidrevics et al., 1993). After 16 years of stagnation, a major inflow transported highly saline water into the Baltic Sea in 1993 (Matthäus, 1993). This inflow is probably partly
responsible for the observed general increase in salinity in the gulf during the following years, although salinity declined in the north-eastern part of the basin in 1998. We suggest that the increase in mesozooplankton stock may partly be attributed to the higher salinity, because the most abundant zooplankton species, particularly some copepods, are euryhaline organisms from marine origin and their distribution in the Gulf of Riga is limited by salinity conditions. The decrease in zooplankton in shallower coastal areas during summer may be partly caused by less favourable feeding conditions in this region. Also, the increase in salinity may reduce the share of zooplankters from freshwater origin, which usually increase in abundance towards the coast.

Concomitant with the increase in copepod abundance and biomass, the declining fraction of empty stomachs in planktivorous herring suggests that feeding activity during the main feeding period has increased. Recent investigations show that clupeids concentrate in deeper areas during periods of low prey density in the region where the seasonal thermocline hits the coastal slope in the north-eastern part. Their feeding activity was significantly higher in this frontal region than in adjacent areas (Ojaveer et al., 1997). Therefore, improved feeding conditions and presumably also better hydrological conditions both have had a direct effect on the feeding activity of pelagic fish in the Gulf of Riga. Sticklebacks tend to remain scattered in warm surface waters and do not form large aggregations in and around the seasonal thermocline. The less pronounced changes in their feeding activity may thus be explained by a different spatial distribution pattern. Also, the feeding strategy of sticklebacks differs from herring. Food composition is more diverse and preferred prey size is smaller.

The significant positive correlation between abundance of \textit{N. integer} and mean winter air temperature suggests that winter severity, which largely determines the heat content of the water mass of the basin, has a marked effect on recruitment of this mysid. The temperature regime probably influences conditions for reproduction. Previous studies on nektobenthos in other parts of the Gulf of Riga have shown that higher abundance and biomass values of \textit{N. integer} were recorded during periods of successive warm summers and after warm winters (Kotta, 1995). One warm summer within a cold period, or a cold summer during a warm period, did not cause any clear changes. However, despite successive warm summers and relatively warm winters, a clear peak in abundance was not observed in the early 1970s. Therefore, other factors, such as the available food resource and predation by fish, must also be partly responsible for the observed variations. During the 1970s and 1980s, eutrophication has resulted in an increase in the overall productivity of Pärnu Bay (Suursaar, 1995), which is the main area for reproduction of \textit{N. integer}. This might partly explain the higher abundance values generally recorded since the late 1980s compared to the 1970s. \textit{N. integer} is also an important prey for several commercially exploited fish species in Pärnu Bay. For instance, its mean share in the diet of smelt, \textit{Osmerus eperlanus} \textit{L.}, has been 40% by weight, but reached even to 67% in 0-group individuals (A. Lankov, unpubl. data, Ojaveer et al., 1997). We compared mean commercial catches of smelt during years of low (1970-1987) and years of high (1988-1996) abundance of \textit{N. integer}. The mean catch of smelt was six times lower during the period of high abundance. Therefore, predation by fish (including pikeperch and herring) might be another important mechanism regulating stock abundance of this mysid in the north-eastern part of the Gulf of Riga.
The presence of cod in the Gulf of Riga depends on the stock size in the eastern Baltic and on the hydrological conditions, particularly in respect of the southern part. According to our data, cod disappeared from the basin during the mid-1980s. However, its sporadic re-appearance in commercial trapnet catches in the Pärnu Bay area in the winter of 1998 is another indication of a shift in the ecosystem of the Gulf of Riga.

Several fish stocks (e.g., sprat, eelpout, scuppins, and sea snail) have declined in abundance since the invasion of cod into the Gulf of Riga at the end of 1970s. Results from stomach analysis have revealed that clupeoids were of major importance in the cod diet. Other fish prey included smelt, eelpout, sandeel, gobies, lumpfish, and butterfish were presented (Bagge, 1981; Uzars, 1994), although the share of other fish did not generally exceed 10% by weight (Uzars, 1975, 1985). Therefore, notable declines in abundance or disappearance of these species from experimental catches during the 1980s might partly be attributed to the impact of cod predation. Since the disappearance of cod from the basin in the mid-1980s, the lack of inflow of saline water into the Baltic (Matthäus, 1993) and the progressive increase in anthropogenic pollution and eutrophication of the basin (Andrushaitis et al., 1995; Suursaar, 1993) have created unfavourable environmental conditions which hamper the recovery of demersal and bentho-pelagic fish stocks (Ojaveer, 1997). In contrast, the pelagic component of the ichthyofauna has shown a clear increase in abundance in the mid-1990s, particularly sprat, but also herring and sticklebacks. From the late 1980s to the mid-1990s, nutrient concentrations in the north-eastern part have dropped markedly (nitrate by a factor of 7, phosphates by 3.5, and silicates by 2.8), indicating that pollution, too, may have decreased (Suursaar and Tenson, 1998). Thus, current changes in the abiotic environment, such as more severe winters, higher salinity, and a decreased anthropogenic impact should enhance marine fish stocks, particularly demersal species preferring a clean and cold-water environment with high oxygen concentrations, including glacial relicts such as the sea snail. The re-invasion of cod into the basin should contribute to the enhancement of the relative importance of the demersal fish component in the system.

The most important recent changes in the ecosystem of the Gulf of Riga are due to changes in the abiotic environment and to the introduction of non-indigenous species transported by ballast water. The changes in the abiotic environment are mostly of natural origin and are caused by fluctuations in the border between two different climate systems (Atlantic and Euro-Asiatic) over the Baltic. However, organisms crossing borders of their original distribution areas by human aid may cause substantial changes in aquatic ecosystems (e.g., Carlton, 1996; Zmudzinski, 1996). The Baltic Sea with its low species diversity and many empty niches in the food web appears especially susceptible to invasion. Our data on the colonization and biomass distribution of *Marenzelleria viridis* in the entire gulf are confirmed by other studies (e.g., Jermakovs, 1998). In contrast, the share of *M. viridis* in the zoobenthic communities is much smaller according to our data. However, the results are not directly comparable because of the different methodologies (e.g., wet and dry weights) applied. With reference to other parts of the Baltic basin, this polychaete is the dominant species in Vistula Lagoon (Zmudzinski, 1996).

*M. viridis* was not found in the Pärnu Bay area and Saaremaa coast before 1994, despite several extensive mapping studies. The larvae cannot complete their development when salinity falls below 5 (George, 1966), which is often the case in the Pärnu Bay coastal area (up to Station 12 m). Perhaps, the improved salinity conditions have favoured the colonization in these areas during recent years. Still, salinity may affect the distribution of *M. viridis* in the gulf, at least in coastal areas. Lehtonen et al. (1998) stated that the competitive ability of this non-indigenous species is probably better than of indigenous dominant benthic invertebrates. This may be another important factor causing recent changes in the zoobenthic communities of the Gulf of Riga.

Information on another newcomer in the pelagic ecosystem of the Gulf of Riga, the cladoceran *Cercopagis pengoi*, has recently been reported elsewhere (Ojaveer, 1997). The distribution area appears to have expanded towards open parts of the Gulf in late summer and then overlaps with the distribution of 0-group smelt. By this time the young smelt have grown big enough to be able to feed on this relatively large prey. Thus, a direct influence through the food web from *C. pengoi* upon the growth, and possibly also year-class strength, of this commercial fish species might be expected.

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References


INTRODUCTION

The paper deals with the influence of various factors on the geographic distribution and abundance of different species of fish in the Väinämöinen region of Finland. The study was conducted by the Institute of Marine Biology, University of Helsinki. The data were collected from various lakes and rivers in the region during the summer months. The results are presented in the following section.

In this paper, we discuss the role of various factors in affecting the distribution and abundance of fish species in the Väinämöinen region. The study was conducted over a period of three years, during which time various environmental parameters were monitored and recorded. The results indicate that several factors contribute to the distribution and abundance of fish species in the region. These factors include water temperature, pH, and the presence of various plants and animals in the ecosystem.
FACTORS AFFECTING THE DISTRIBUTION, ABUNDANCE AND BIOMASS OF INVERTEBRATE FAUNA IN THE VÄINAMERI (NORTH-EASTERN BALTIC SEA)

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ABSTRACT

The relationships between the abundance and biomass structure of invertebrate assemblages and various environmental variables were sought by using multivariate statistics. No key variable determining the structure of macrozoobenthos in the whole Väinameri Sea was found. Sediment type explained the biggest part of the variation in invertebrate assemblages in the deeper areas and dominant macroalgal species in the shallower areas. Additionally, the loose-lying macroalgae, Furcellaria lumbricalis, contributed to the increase in macrozoobenthos densities in the deeper parts of the Väinameri by offering secondary substrate for true hard bottom invertebrates. The infauna below the algal mat was poorer as compared to the sediments in unvegetated areas. On the other hand, the introduced polychaete, Marenzelleria viridis, was found only under the mat of F. lumbricalis and the biomass of the polychaete increased with the coverage of F. lumbricalis.

Key words: algal mat, Baltic, Furcellaria, macrozoobenthos, Marenzelleria

1. INTRODUCTION

The Baltic Sea is one of the world’s largest brackish water basins. Owing to the salinity constraints, short developing time and isolation, the number of benthic species in the Baltic fauna is low as compared to other brackish water ecosystems (Segerstråle 1957). High level of urbanisation and industrialisation further reduces biodiversity (Gray 1997) as well as the functioning efficiency and resistance of the system (Naeem et al. 1994). On the other hand, low species richness and intensified human influence have resulted in a number of successful introductions of alien species into the Baltic Sea in recent years (Jansson 1994). The examples of invasions in the 1980s and 1990s have shown that successful exotics may render a previously stable system unbalanced and unpredictable (Mills et al. 1993, Carlton 1996, Leppäkoski 1991) and similarly to eutrophication may severely affect biological diversity in the area (Gollasch & Leppäkoski 1999). In that respect, the Baltic Sea is in strong need of conservation. In order to conserve the
system, managers must have an understanding about the forcing factors of an ecosystem and how the ecosystem will be altered by changes in climate and human activity.

The Väinameri Sea contains a large number of different habitats and has a singularly high benthic diversity as compared to other regions in the north-eastern Baltic Sea (Järvekülg 1970). An extensive part of the Väinameri is covered by a unique assemblage of a loose-lying macroalgae *Furcellaria lumbricalis* Lamour (Trei 1970). In spite of the fact that the invertebrate and macro-algal assemblages are relatively well described (Järvekülg 1970, Trei 1970) the mechanisms and driving forces that contribute to the benthic diversity are not known.

In this study we examined the role of some environmental variables in the variability of macrozoobenthos in the Väinameri region. Relationships between sediment type, depth, the content of nutrients in water, water transparency, phytobenthos and the abundance and biomass structure of benthic invertebrate assemblages were sought by using multivariate statistical programs. Special attention was paid to the factors that structure the faunal composition of *F. lumbricalis* assemblage. A key question to be answered here is whether an algal mat increases or reduces the benthic diversity in the area? Among positive effects, *F. lumbricalis* should increase sediment stability and habitat complexity and at the same time reduce fish predation. On the other hand, *F. lumbricalis* may facilitate the development of temporary anoxic conditions and prevent larval settlement in the sediment below the algal mat.

### 2. MATERIAL AND METHODS

The Väinameri Sea (Fig. 1) cannot be regarded as a single water mass with the same hydrophysical properties throughout (Suursaar *et al.* 1998). Kassari Bay is often separated by sub-fronts from the eastern part of the Väinameri and the Baltic Sea proper. The region is on average more saline (7 psu) as compared to the eastern part of the Väinameri (6 psu) due to the frequent inflows of saline water through the Soela Strait. The major part of Kassari Bay is covered by a loose-lying macroalgae *F. lumbricalis* community (Trei 1970). The community is maintained by the prevailing circular currents and the grid of islets that surround Kassari Bay.

Depending on the season the eastern section of the Väinameri is influenced either by eutrophied water of the Gulf of Riga (autumn and ice-free winter) or the cleaner water of the Baltic Sea proper (summer) (Suursaar *et al.* 1998). Sand and sandy clay substrates prevail in the major part of the study area. Average depth is below 10 m (Mardiste 1970).

Macrozoobenthos was sampled from 20 stations in the whole Väinameri and from 20 stations in Kassari Bay (uniform sampling design for both) during August 1995. Samples were collected with a Tvärminne sampler (catching surface 315 cm², Kangas 1972) on silty, sand or gravel bottoms and with a suction sampler (catching surface 315 cm², Hiscock & Hoare 1973) on boulders and limestone. Samples below 0.5 m were taken by SCUBA diving. Three random samples were taken from each site. In order to better distinct infauna and the species associated to free-floating algae in Kassari Bay the samples were split before sieving into two parts: the layer of *F. lumbricalis* and sediment. During sampling the sediment type (stone, boulder, pebble, gravel, coarse sand, medium sand, fine sand, silt, clay or mixed), depth,
coverage of phytobenthos, dominant species and thickness of algal canopy were recorded. The average values of salinity, the content of nutrients and water transparency were obtained from the literature (Suursaar et al. 1998).

Material was sieved through a net of 0.5 mm mesh size and then deep frozen at -20°C. In the laboratory animals were counted under a binocular microscope. Dry weights were obtained (to the nearest 0.1 mg) after drying the material at 70°C for 60 hours.

For multivariate data analyses the package PRIMER was used (Clarke & Warwick 1994). The Bray-Curtis similarity measure was used in cluster analysis. Prior to the analysis data were double square root transformed to reduce the contribution of abundant species to similarity measure. ANOSIM permutation test (Clarke & Green 1988, Clarke 1993) gave the significance level of differences in the community structure of macrozoobenthos between predefined groups (i.e. different sediment types and phytobenthic communities). The contribution of species to the similarity within the defined groups and dissimilarities between the groups were investigated using the SIMPER procedure (Clarke 1993). BIO-ENV test was used to demonstrate the importance of different environmental variables in determining the structure of macrobenthic assemblages in the area.

3. RESULTS

According to non-metric multidimensional scaling (MDS) benthic invertebrate assemblages did not form clearly distinguished groups in terms of abundance and biomass structure (Fig. 2). In order to identify the environmental factors that were most strongly related to the variability of benthic invertebrate assemblages BIO-ENV analysis was run. The effect of environmental variables was similar on both abundance and biomass structure of macrozoobenthos (Table 1). Among abiotic variables depth gave the best match with the structure of invertebrate assemblages. There was a significant difference in macrozoobenthos assemblages between 0–4 m and 4–10 m. Among biotic variables the type of vegetation was the most important variable.

In the deeper areas (> 4 m) of the Väinameri the sediment type explained the biggest part of the variation in the invertebrate abundance and biomass structure (BIO-ENV Spearman rank correlation coefficient 0.154 for abundance and 0.151 for biomass), whereas the dominant macroalgae (0.456 for abundance, 0.253 for biomass) was the key variable in the shallower areas (≤ 4 m).

Macrobenthic communities on stone bottoms clearly opposed other sediment types. There were significant differences between stone and coarse sand (ANOSIM, p=0.01), silt (p=0.04), silty clay (p=0.02), clayey sand (p=0.03) and clay bottoms (p=0.05). However, no significant differences were observed for biomasses except between the coarse sand and clayey sand bottoms (p=0.05).

Stone bottoms were characterised by high abundances of Gammarus spp. (2461 ± S.E. 1101 ind m⁻²), Mytilus edulis L. (1574 ± 971 ind m⁻²), Hydrobia spp. (2270 ± 1746 ind m⁻²) and Theodoxus fluviatilis L. (945 ± 619 ind m⁻²); pebbly sand and silt by Hydrobia spp. (2088 ± 1304, 8928 ± 6881 ind m⁻²); silty sand by Lymnaea peregra (O. F. Müller) (1450 ± 1014 ind m⁻²); fine sand by Hydrobia spp.
(5816 ± 3644 ind m\(^{-2}\)) and *Macoma balthica* L. (1437 ± 580 ind m\(^{-2}\)). Coarse sand, medium sand, clayey sand and clay bottoms had moderate abundance of *M. balthica* (545 ± 340, 193 ± 58, 551 ± 221 and 837 ± 401 ind m\(^{-2}\)). Besides, coarse and medium sand bottoms had moderate density of *Hydrobia* spp. (603 ± 261, 537 ± 293 ind m\(^{-2}\)) and *M. edulis* (150 ± 110, 906 ± 315 ind m\(^{-2}\)), clayey sand *Cerastoderma glaucum* Bruguière (310 ± 193 ind m\(^{-2}\)) and clay bottoms *M. edulis* (176 ± 112 ind m\(^{-2}\)) and *Mya arenaria* L. (239 ± 140 ind m\(^{-2}\)).

According to the biomass of macrozoobenthos, different sediment types were relatively similar. The dominant species were *M. edulis*, *M. balthica* or *M. arenaria*. Depending on the type of substrate, subdominants were *C. glaucum*, *L. peregra* or *Hydrobia* spp. As to clayey sand and coarse sand bottom, the former had a higher biomass of *M. balthica* (29 ± 8 vs. 19 ± 11 g m\(^{-2}\)) and *C. glaucum* (20 ± 18 vs. 0 g m\(^{-2}\)) and a lower biomass of *M. arenaria* (1 ± 0.3 vs. 20 ± 19 g m\(^{-2}\)) and *M. edulis* (0 vs. 3 ± 2.8 g m\(^{-2}\)).

*F. lumbricalis* was the most prevalent phytobenthos species in the Väinameri followed by *Pilayella littoralis* Kjellm. and *Fucus vesiculosus* L. Macrozoobenthic communities on *F. vesiculosus* and *F. lumbricalis* significantly differed from each other (ANOSIM, abundance at *p* = 0.01 and biomass at *p* = 0.04). No other differences were significant. *F. vesiculosus* community had a higher abundance of gammarids (483 ± 118 ind m\(^{-2}\)) and *Hydrobia* spp. (1547 ± 1305 ind m\(^{-2}\)) and a lower biomass of *M. balthica* (6 ± 4.8 g m\(^{-2}\)). *F. lumbricalis* community had a higher abundance and biomass of *M. edulis* (2007 ± 423 ind m\(^{-2}\), 26 ± 6 g m\(^{-2}\)).

When only *F. lumbricalis* assemblage was concerned (Kassari Bay) ANOSIM test showed a clear difference between macrozoobenthos in vegetation and the sediment below (*p* < 0.05) as well as between vegetated and unvegetated patches (*p* < 0.001).

The type of sediment and coverage of *F. lumbricalis* explained most of the variability in invertebrate abundance (BIO-ENV Spearman rank correlation coefficient 0.267 and 0.203 for sediment and coverage, respectively) and biomass (0.243, 0.065) structure in Kassari Bay. The layer of *F. lumbricalis* was characterised by a high abundance and biomass of *M. edulis*. The biomass of *M. edulis* increased with the coverage of *F. lumbricalis* (Fig. 3).

*M. balthica* was the most prevalent species in the sediment. *C. glaucum*, *M. arenaria* and *Marenzelleria viridis* (Verrill) inhabited only sediments and were never found in the mat of *F. lumbricalis*. There was no difference in the infaunal species composition between unvegetated and vegetated patches. However, the abundance and biomass values of infauna were related to the thickness of the *F. lumbricalis* mat, being lower in more densely vegetated areas (Fig. 4). As an exception, the biomass of *M. viridis* increased with the coverage of *F. lumbricalis* (Fig. 5).

### 4. DISCUSSION

No key environmental variable structuring the macrozoobenthos of the Väinameri Sea was found, indicating both hydrodynamic instability and diversity of the system. Sediment had the most important influence on the structure of invertebrates in the deeper areas and benthic vegetation in the shallower areas.
Due to the intensive currents and stochastic storm events sediment is highly mobile in the shallower parts of the study area (Mardiste 1970, Suursaar et al. 1998). In that respect, macrophytes are able to offer benthic invertebrates refuge from sediment mobility and, hence, control the standing stock and diversity of macrozoobenthos (e.g. Reusch & Chapman 1995).

In the deeper areas where the sediments are more stable, the structure of macrozoobenthos is mainly determined by the properties of substrate — either primary substrate or the type of algal canopy. The loose lying *F. lumbricalis* highly contributes to the increase in the biomass of macrozoobenthos by offering the appropriate substrate for true hard bottom species, for example *M. edulis*.

We expected that the overall effect of *F. lumbricalis* on macrozoobenthos inhabiting the sediment below the algae to be positive both through increased sediment stability and decreased fish predation. However, our results demonstrated that the infaunal density did not increase with the thickness of *F. lumbricalis*. On the contrary, the densities were greater in unvegetated areas as compared to vegetated areas.

The space is not considered as a limiting factor for benthic assemblages in soft sediments (Levinton, 1972). It is likely that due to considerable biodeposition of the filter-feeding community (e.g. Kautsky & Evans 1987, Kotta et al. 1998), the food is not limiting the infauna in the area either. Hence, lower biomass values of benthic invertebrates under *F. lumbricalis* may be due to the decomposition of epiphytic filamentous algae attached to *F. lumbricalis* resulting in temporary hypoxic conditions. Besides, a significant amount of organic matter is directed into the benthic system through the biodeposition by *M. edulis*. Consequent decay of the biodeposits may further deteriorate the oxygen regime. Similar negative effect of drifting algae (here detached filamentous algal mats) on benthic invertebrates has been previously documented elsewhere in the Baltic Sea (e.g. Norkko & Bonsdorff 1996ab). These studies demonstrated that in most severe cases the algal mats may wipe off all infauna and significantly reduce benthic invertebrates associated to the algae. Nevertheless, we believe that this will never happen in Kassari Bay owing to the coarse structure of *F. lumbricalis* and high hydrodynamic activity in the area.

It is rather interesting that the region where the introduced polychaete, *M. viridis*, was found in the Väinameri coincided with the distribution area of *F. lumbricalis*. The species was for the first time observed in the Baltic in 1985 (Bick & Burckhardt 1989), and since then it has spread quickly around the whole Baltic Sea (Essink & Kleef 1993, Kotta & Kotta 1998). Higher biomass of the polychaete under the mat of *F. lumbricalis* agrees with the hypothesis that low predation and uniformity of assemblage facilitate the establishment of introduced species (Carlton 1996). Besides, intermediate disturbance (Connel 1978) due to temporary hypoxia may be beneficial for the establishment of opportunistic species like *M. viridis*.

To conclude, biotic variables were superior over abiotic variables in describing the abundance and biomass structure of macrozoobenthic assemblages in the Väinameri. Due to the hydrological instability of the system, the distribution of macrozoobenthos is related to the availability of refuge in the shallower areas and both to the availability of food and the properties of the loose-lying *F. lumbricalis* in the deeper areas. Occasional development of hypoxic conditions may have an adverse influence on the infauna living under *F. lumbricalis*, which at the same time may facilitate the establishment of the introduced polychaete *M. viridis*. 

5
ACKNOWLEDGEMENTS

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REFERENCES


Table 1. Results of BIO-ENV analysis: the values of Spearman rank correlation coefficient between different environmental variables and the abundance and biomass structure of macrozoobenthic assemblages

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Abundance</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (Pos N)</td>
<td>-0.016</td>
<td>-0.061</td>
</tr>
<tr>
<td>Longitude (Pos E)</td>
<td>0.054</td>
<td>-0.002</td>
</tr>
<tr>
<td>Sediment</td>
<td>0.105</td>
<td>0.084</td>
</tr>
<tr>
<td>Depth</td>
<td>0.118</td>
<td>0.112</td>
</tr>
<tr>
<td>N tot in water</td>
<td>0.051</td>
<td>-0.013</td>
</tr>
<tr>
<td>P tot in water</td>
<td>0.050</td>
<td>-0.012</td>
</tr>
<tr>
<td>Water transparency</td>
<td>0.051</td>
<td>-0.013</td>
</tr>
<tr>
<td>Dominant macroalgae in the sample</td>
<td>0.195</td>
<td>0.195</td>
</tr>
<tr>
<td>Dominant macroalgae at the site</td>
<td>0.131</td>
<td>0.111</td>
</tr>
<tr>
<td>Coverage of macroalgae at the site</td>
<td>0.085</td>
<td>0.004</td>
</tr>
</tbody>
</table>
Figure 1. Study area. The stars represent the grid of sampling stations in the whole Väinameri area and the crosses that of Kassari Bay, respectively.
Figure 2. MDS ordination on the double square root transformed abundance (upper figure) and biomass (lower figure) data of macrozoobenthos. Arrows indicate the gradients of the most important environmental factors.
Figure 3. The relationship between the coverage of *F. lumbricalis* and the biomass of *M. edulis* in Kassari Bay in 1995.

\[ y = 0.0024x^2 + 0.2268x + 1.2341 \]
\[ R^2 = 0.4647 \]

Figure 4. The relationship between the coverage of *F. lumbricalis* and the biomass of infauna in Kassari Bay in 1995.

\[ y = 0.0227x^2 - 3.5664x + 156.13 \]
\[ R^2 = 0.6401 \]
Figure 5. The relationship between the coverage of *F. lumbricalis* and the biomass of *M. viridis* in Kassari Bay in 1995.

\[
y = 0.0002x^2 - 0.0017x + 0.1233 \\
R^2 = 0.6294
\]
ABSTRACT

The distribution of shallow water (0-1.5 m) sediments in the coastal region of the Gulf of Aqaba is described in relation to selected physical, chemical, and biological parameters. The type of accommodation and the nature of the sediments in this area, as well as their influence on the biota, are discussed.

I. INTRODUCTION

The Gulf of Aqaba (Arabic Sea) is a shallow-water basin and has low salinity values compared to the Red Sea. This area is characterized by its high diversity of species. The Gulf is surrounded by the major continental areas of the Indian Ocean and the Red Sea. However, the Gulf is isolated from the Indian Ocean by the Letho barrier. It is therefore considered to be a separate entity.

The aim of this study is to investigate the distribution of shallow water sediments in the Gulf of Aqaba and their relationship to physical, chemical, and biological parameters. The results of this study will be compared to those of previous studies in the Gulf of Aqaba.
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Benthic faunal assemblages
in the shallow water areas of the Gulf of Riga (manuscript).
BENTHIC FAUNAL ASSEMBLAGES IN THE SHALLOW WATER AREAS OF THE GULF OF RIGA

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key words: Baltic Sea, distribution, macrozoobenthos, phytobenthos

ABSTRACT

The distribution of shallow water (0.1–6 m) macrozoobenthic assemblages of the Gulf of Riga is described in relation to salinity, depth, sediment type and phytobenthos. The type of macrovegetation describes most of the variability in both abundance and biomass structure of zoobenthos assemblages. Next important factors are salinity and sediment type. Owing to the nutrient load from rivers, macrobenthic assemblages show signs of deterioration adjacent to the Daugava River and the inner part of Pärnu Bay. Macrozoobenthos in other regions is typical of the clean areas of the northern Baltic Sea. As compared to the situation in the 1960s no substantial increase in the abundance and biomass values of macrozoobenthos was observed.

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1. INTRODUCTION

The Gulf of Riga (Baltic Sea) is a relatively shallow and closed water basin characterized by a fairly high riverine input from the extensive drainage area. The gulf is considered to be one of the most eutrophied areas in the Baltic (SUURSAAR, 1995; OJAVEER, 1997). However, in the early 1990s, because of economic recession in Estonia and Latvia, nutrient discharges into the gulf fell substantially (STÅLNACKE et al., 1999) and, hence, the ecosystem is expected to recover.

The state of the aquatic environment has often been assessed via macrobenthic organisms because they are long-lived, sessile, easy to collect and determine (e.g. LEPPÄKOSKI, 1975; HELCOM, 1993). Earliest quantitative surveys of benthic invertebrates in the Gulf of Riga were carried out in the 1950s (SHURIN, 1953, 1960, 1961). These investigations were followed by the profound studies by JÄRVEKÜLG (1961, 1962, 1979). Both series of investigations were mainly concentrated on the macrobenthos inhabiting soft substrate, i.e. deeper parts of the basin. Since then no concise work about the macrozoobenthos of the whole gulf has been published and most papers deal with the impact of the Pärnu or Daugava rivers (e.g. LAGZDINSH, 1975;
Hence, the extensive coastal areas of the Gulf of Riga have been almost overlooked in terms of macrozoobenthos.

The objective of this investigation is to provide the first quantitative data on the distribution of benthic invertebrates in the whole coastal sea of the Gulf of Riga. The coastal zone controls exchange, storage and transformation processes of materials; hence, knowledge about the structure and function of benthic assemblages in this zone is fundamental to our understanding of the system functioning as a whole. Scuba diving made it possible to describe quantitatively the zoobenthic assemblages on hard substrate and helped better distinguish true sediment and macrophyte dwelling species. The distribution of benthic invertebrates is related to environmental parameters such as sediment type, depth, salinity and benthic vegetation. The last has been neglected from most studies dealing with shallow water benthic fauna. Finally, the results will be compared with the historical data on the area.

2. MATERIAL AND METHODS

Sampling was performed in August 1995 and 1996 on 10 transects located around the whole coastline of the Gulf of Riga (Fig. 1). The northern part of the gulf is characterized by a wide coastal zone with diverse bottom topography and macrophyte community, and the southern side by a narrower sandy coastline and hard bottom substrate in the deeper parts of the littoral zone.

Samples were collected with a Tvärminne sampler (KANGAS, 1972) on sand and gravel bottoms and a suction sampler (HISCOCK and HOARE, 1973) on hard bottom types such as boulders and limestone. The sampling area is 314 cm² in both samplers. In general three samples were taken from 32 sites (total 94 samples), of which 19 were unvegetated (56 samples), 6 sites had vascular plants (18 samples) and 7 sites algal (filamentous algae, Fucus vesiculosus L. or Furcellaria lumbricalis J. V. Lamour) vegetation (20 samples). The sampling depth varied from 0.1 to 6.0 m. Samples below 0.5 m were taken by SCUBA diving. Sampling sites were chosen to cover all possible sediment types and macrophytobenthic communities in the transect.

In each site the type of substrate (stone, boulder, gravel, sand, silt, clay or mixed), depth and dominant plant species were recorded. Annual minimum values of salinity and annual maximum content of chlorophyll a were estimated from the data published by Tenson (1995), Berzinsh (1995) and from the data collected in spring 1995 (Wassmann, 1996).

Material was sieved through a net of 0.5 mm mesh size and preserved in 4% buffered seawater formaline solution. In the laboratory animals were counted under binocular microscope. Dry weights were obtained (to the nearest 0.1 mg) after drying the material at 70 °C for 60 hours. Molluscs were weighed with shells.

The contribution of site, sediment type and dominant phytobenthic species on the abundance and biomass of macrozoobenthos was tested by one-way ANOVA after checking for normality of the data (Kolmogorov-Smirnov test for goodness of fit) and homogeneity of variance (Bartlett's, Hartley's tests) (Sokal and Rohlf, 1981).

Multivariate data analyses were performed by statistical package “PRIMER” (Clarke and Warwick, 1994). In order to increase the signal-to-noise ratio in the multivariate analysis an average of three replicates in each site was used to construct
similarity matrices. Bray-Curtis similarity measure was used. Data were log-transformed to reduce the contribution of abundant species to similarity measure. Ordination was made by nonmetric multidimensional scaling (MDS) (Clarke and Green, 1988). The statistical differences in invertebrate assemblages between defined groups were obtained by ANOSIM permutation test (Clarke and Green, 1988; Clarke, 1993). The contribution of each species to dissimilarities was investigated using the similarities percentages procedure (SIMPER) (Clarke, 1993).

3. RESULTS

The total abundance and biomasses of macrozoobenthos varied strongly between the transects of the study area (Fig. 1). The highest mean abundances were found in the outermost part of the Gulf of Riga (transect 4; 5838 ind m\(^{-2}\)) and the lowest on the adjacent area across the Irbe Strait (transect 9; 71 ind m\(^{-2}\)); the highest mean biomasses were recorded in the easternmost part of the gulf (transect 6; 71 g dry wt. m\(^{-2}\)) and the lowest adjacent to the Daugava River and in the coastal sea of Ruhnu Island (transects 7 and 10, respectively; 7 g dry wt. m\(^{-2}\) in both regions). The distribution pattern of abundance and biomass values along the depth gradient was not consistent. Depending on the location of the transect denser populations were observed in shallower areas (transects 4, 5), at moderate depths (transects 1, 2, 7, 8, 9) or in deeper areas (transects 3, 6, 10).

Species composition, abundance and biomass varied between different bottom and vegetation types (Fig. 2). Vascular plant communities were characterized by higher abundance of insects and gastropods of freshwater origin (Lymnaea sp., Bithynia tentaculata (L.)), while the biomass was dominated by burrowing mussels (Macoma balthica L. and Cerastoderma glaucum Bruguère).

Unvegetated bottom types were dominated by crustaceans (mainly Gammarus spp. and Corophium volutator (Pallas)), polychaetes (Nereis diversicolor (O. F. Müller) and Marenzelleria viridis (Verrill)) and oligochaetes. The abundances were highest in shallow (< 1 m) sandy bottoms in the north-eastern part of the gulf (3700 ind m\(^{-2}\)) while the shallow areas of the south-eastern part had very low numbers of macrofauna (only 160 ind m\(^{-2}\)). The biomass was mainly composed by burrowing mussels, M. balthica and C. glaucum in shallow areas and M. balthica and Mya arenaria L. in deeper and coarser bottoms. The biomass was highest in deep (5–6 m) gravel bottoms (76 g dry wt. m\(^{-2}\)).

Hard bottom algal communities consisted mainly of Theodoxus fluviatilis (L.), Jaera albifrons coll. Leach, Idotea chelipes (Slabber), I. baltica (Pallas), Gammarus spp. and sedentary mussels, Dreissena polymorpha (Pallas) and Mytilus edulis L. In four sites the last mentioned two mussel species were found in the same samples.

We distinguished five different trophic groups of macrozoobenthos: omnivores, detritivores, carnivores, herbivores and filter-feeders (Fig. 3). Detritivores contributed significantly to the total abundance in the northern part of the gulf (mainly M. balthica) whereas omnivores were much more abundant in the southern part of the gulf (Oligochaeta, Gammarus spp.). The proportion of herbivores was higher in the eastern part of the gulf (T. fluviatilis in the south-eastern part and Hydrobia spp. and Lymnaea spp. in the north-eastern part of the gulf). Considering biomasses, detritivores were still
the dominant type in the northern part of the gulf (M. balthica), with a significant proportion of filter-feeders in the vicinity of Pärnu Bay (D. polymorpha). Different feeding types had similar proportions in the southern part of the gulf. The proportion of filter-feeders was higher on transects 6 and 8. Transect 6 has a unique position representing either the communities of northern type (by biomass) or southern type (by abundance).

Salinity seems to be an important variable in determining the structure of macrozoobenthos communities in the Gulf of Riga (Fig. 4). Dividing the community into 3 groups (marine, brackish and fresh water species) we may see higher proportion of brackish and fresh-water species in the southernmost part (transects 7 and 8) and north-easternmost part of the gulf (transect 2). These transects are influenced by the inflow of either the Daugava or the Pärnu river.

According to one-way ANOVA (Table 1), sediment type affects the abundance values of macrozoobenthos whereas the dominant plant species is significant in describing both the abundance and biomass values of macrozoobenthos. Higher abundances were found on stone, sandy gravel and gravelly clay bottoms, the lowest on clayey sand and sand bottoms. The lowest abundances and biomasses were found on Zannichelia palustris L. community, the highest on F. vesiculosus and Cladophora rupestris Kütz. communities. The density of herbivores and omnivores was significantly higher on stone bottoms, detrivores on sandy gravel and gravelly clay bottoms. Filter-feeders preferred F. vesiculosus, F. lumbricalis and Myriophyllum spicatum L. dominated communities, herbivores F. vesiculosus community, carnivores F. lumbricalis and M. spicatum communities and omnivores C. rupestris and F. vesiculosus communities. The abundance and biomass of detrivores were independent of the type of plant communities around the sampling area.

Ordination of log-transformed macrozoobenthos abundance and biomass data did not produce well-distinguished groups (Figs. 5 and 6). Considering biomass values transect 2 is clearly distinguished from transects 8, 9 and 10 (ANOSIM, p < 0.05), transect 3 from transects 8 and 9 (p = 0.03) and transect 4 from transect 7 (p = 0.03). Most of the dissimilarities are due to M. balthica, C. glaucum, B. tentaculata, N. diversicolor, D. polymorpha and T. fluviatilis. The first three species have higher biomasses in the northern part of the gulf. T. fluviatilis, on the contrary, is more common in the southern coasts of the gulf. D. polymorpha thrives in the north-eastern and southern coasts whereas N. diversicolor occurs in higher biomasses in the western side of the gulf. As to the ordination of macrozoobenthos by abundance, transects are even more similar to one another.

Despite the significant variation in the proportion of marine, brackish and fresh-water species in the study area, salinity values practically did not contribute to the ordination pattern. Surprisingly, only a weak relationship was found between bottom types and the structure of macrozoobenthos communities. Significant differences were observed comparing very different substrate types such as stone bottoms with gravel-sand bottoms (ANOSIM, p < 0.01). Stone bottoms were characterized by higher densities of D. polymorpha, T. fluviatilis, Turbellaria, Gammarus oceanicus Segerstråle, G. salinus Spooner, G. zaddachi Sexton et Spooner and C. glaucum. Much higher abundances of M. viridis and Oligochaeta were observed on gravel-sand bottoms.

Taking into account the dominant phytobenthos species in the sampling site, we estimated the relationship between the distribution of the dominant algal species and the structure of macrozoobenthos communities. There was a significant difference between
the areas devoid of vegetation and \( Z. \) palustris community (calculations based on macrozoobenthos biomass data, ANOSIM, \( p = 0.05 \)) and between \( F. \) vesiculosus and \( Potamogeton \) pectinatus L. communities (abundance data, \( p = 0.03 \)). In the former case, \( T. \) fluviatilis, \( M. \) balthica and \( N. \) diversicolor contributed to the differences between these two community types. The last two species had higher biomasses on unvegetated areas and \( T. \) fluviatilis in the \( Z. \) palustris community. Comparing \( F. \) vesiculosus and \( P. \) pectinatus communities \( J. \) albifrons coll., \( Gammarnus \) spp., \( T. \) fluviatilis, \( I. \) viridis and \( M. \) balthica had higher abundances in the \( Fucus \) belt whereas only the Chironomidae of \( P. \) pectinatus community outnumbered those of \( F. \) vesiculosus community.

4. DISCUSSION

The abundance and biomass values of macrozoobenthos found in this study are in the same magnitude as found in other coastal areas in the northern Baltic Sea (\textit{e.g.}\ Elmgren and Ganning, 1974; Skult, 1977; Orav and Kotta, 2000). However, the biomasses found in the Gulf of Riga were much lower than those in the Baltic Proper. This corresponds to the decline of \( M. \) edulis population due to lower salinity values in the Gulf of Riga.

Analysing the dispersion and structure of phytobenthic communities in the Gulf of Riga \textit{KAUTSKY et al.} (1999) found the highest animal biomasses, up to 200 g dw m\(^{-2}\), in the southernmost part of the gulf, while elsewhere the mean values were around 40–50 g dw m\(^{-2}\). Our study showed about the same values also for unvegetated areas. This means that both macroalgal communities and unvegetated areas play an important role as storages of overall matter and energy in the littoral zone of the Gulf of Riga.

The functional group approach has been considered more indicative and of general importance than studies of individual taxa (\textit{BEGON et al.,} 1996). Higher proportion of filter-feeders in the north-eastern part of the Gulf of Riga indicates a relatively important inflow of nutrients from the Pärnu River. Thus, besides salinity eutrophication may be considered a very important factor in structuring the zoobenthic communities in Pärnu Bay. Although the water treatment plant of the town of Pärnu was launched in 1992, the high density of mussels indicates that there is still considerable effort to be made to improve the water quality in Pärnu Bay. On the other hand, there is evidence that after the shutdown of the sewage pipeline a very abundant filter-feeder community may persist in the area over a decade (Kotta, I. and J. Kotta, 1997).

The proportion of filter-feeders was fairly low in the vicinity of the Daugava River, the main pollution source of the Gulf of Riga (transect 7). At the same time a very strong increase in the abundances and biomasses of filter-feeders (mainly \( D. \) polymorpha) was observed on both sides of the estuary of the Daugava River (transects 6 and 8). Lack of filter-feeders in the vicinity of the Daugava River may be considered as an artefact and it reflects the prevalence of soft substrate in the area, which is not suitable for \( D. \) polymorpha.

Higher biomasses of detritivores in the northern part of the gulf are related to a different coastal morphology. Because of the wider littoral zone and lower input of wave energy, sedimentation bottoms are more common in the northern part as compared to the southern part of the gulf. Hence, the development of dense populations of \( M. \) balthica is favoured in the north.
The numerical prevalence of omnivores in the southern part of the Gulf of Riga may be related to lower salinity values as Chironomidae and Oligochaeta could be mentioned as the most abundant omnivores. However, we should also mention the healthy phytobenthic communities that supported numerous Gammarus spp. populations. Although Gammarus spp. were important in the vegetated areas of the northern parts of the Gulf of Riga (mainly coastal sea of Saaremaa Island) they had little importance in the overall abundance and biomass figures as compared to thriving mollusc populations.

Comparison of the proportion of macrozoobenthos of different feeding types in unvegetated and vegetated areas showed that vegetated areas had a much smaller proportion of filter-feeders in the vicinity of the Daugava and Pärnu rivers while in the coastal sea of Saaremaa Island the proportion of filter-feeders was small in unvegetated areas. There was no significant difference in other feeding types between vegetated and unvegetated areas.

Based on the phytobenthos communities, Kaustky et al. (1999) divided the Gulf of Riga into five different sub-areas: Pärnu Bay and the adjacent sea (A, transects 1-3), southern coastal areas of Saaremaa Island (B, transects 4-5), middle part of the eastern and western gulf (C, transects 6, 9), southernmost gulf and coastal sea of Ruhnu Island (D, transects 8, 10) and finally the vicinity of the Daugava River (E, transect 7).

We used a similar grouping while running the ANOSIM of log-transformed macrozoobenthos abundance and biomass data (Table 2, Figs. 5, 6). Our findings indicate that the grouping of macrozoobenthos (especially when considering biomass values) based on the whole phytobenthos community leads to better results than the grouping based only on the dominant algal species. Two clear groups of communities could be distinguished: northern (including plant communities A and B; characterized by a higher proportion of annual plants and Magnoliophyta; among zoobenthos detritivores are more important) and southern type (C, D; higher proportion of perennial plants and Cladophora glomerata Kütz; omnivores are more important).

The differences between the communities in the vicinity of the Daugava estuary (E) and other southern coastal sea areas were not always evident. Taking into account the biomasses, the zoobenthos in the vicinity of the Daugava River was of an intermediate type between the northern and southern areas of the Gulf of Riga. Considering abundances, the stations of the Daugava transect were placed in the extreme ends of the ordination plot.

To conclude, the factors most significantly related to the variability of benthic invertebrate assemblages were vegetation type followed by salinity and sediment type. However, the effect of different factors was often interrelated and difficult to separate.

According to Järvekülg (1961, 1979) M. balthica dominated the whole sublittoral zone of the Gulf of Riga in the 1960s. This is also true, nowadays, with the minor local exceptions where M. viridis, N. diversicolor, D. polymorpha or T. fluviatilis may take the leading role. Due to the differences in methodology it is hard to compare the changes in species diversity. However, earlier studies have demonstrated the decline of phytophilous species in the northern part of the Gulf of Riga (Kotta, J. and I. Kotta, 1997).

In the 1960s the average abundance and biomass values were respectively 840 ind m⁻² and 3 g wet weight m⁻² between 0.1 and 0.4 m and 2210 ind m⁻² and 62 g wet weight m⁻² between 0.5 and 9 m (Järvekülg, 1979). We measured 2640 ind m⁻² and 18 g dry weight m⁻² in the shallower areas and 2475 ind m⁻² and 35 g dry weight m⁻² in the deeper areas, respectively. The average ratio of wet weight to dry weight in the
study area was about 2.8. Figure 7 compares the average abundance and biomass data of macrozoobenthos at different sediment types between the 1960s and this study. As the methods used by Järvekülg underestimated the abundances and biomasses of macrozoobenthos on stone and gravel bottoms (most prevalent at 0.1–2 m) the magnitude of the changes was smaller than shown above. Hence, it is likely that the biomass and abundance of macrozoobenthos have not increased significantly in the coastal sea of the Gulf of Riga during the last 30 years.

5. CONCLUSIONS

On the basis of macrozoobenthos assemblages, the Gulf of Riga may be broadly divided into southern and northern areas. Among abiotic variables sediment, salinity and locally nutrient input by rivers explain a significant proportion of the variation in the abundance and biomass of macrozoobenthos. The dispersion of macrophytobenthos should be taken into account as a key variable explaining the majority of the structure of macrozoobenthos assemblages in the Gulf of Riga. The biomass and abundance of macrozoobenthos have not substantially increased during the last 30 years. The overall condition of macrozoobenthic assemblages seems to be good compared with similar areas in the Northern Baltic Sea.

6. ACKNOWLEDGEMENTS

The study was carried out within the framework of the littoral project of the Gulf of Riga financed by the Nordic Council and partly by Estonian Governmental Programme no 0200792s98. We thank the crew of R/V Marina for their assistance in the field work.

7. REFERENCES


Table 1. One-way ANOVA of effects of sediment and vegetation types on abundance and biomass values of different trophic groups of benthic invertebrates

<table>
<thead>
<tr>
<th>Model</th>
<th>Total</th>
<th>Filter-feeder</th>
<th>Herbivore</th>
<th>Carnivore</th>
<th>Detrivore</th>
<th>Omnivore</th>
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<td>Sediment</td>
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<td>&lt;0.001</td>
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<td>&lt;0.001</td>
<td>0.988</td>
<td>0.209</td>
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<td>Vegetation</td>
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<td>0.001</td>
<td>&lt;0.001</td>
<td>0.202</td>
<td>0.660</td>
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<tr>
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<td>Biomass</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.170</td>
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</table>

Table 2. Results of pairwise tests from one-way ANOSIM (log-transformed abundance and biomass data). Division into the groups is based on the results of the grouping of macrophytobenthos assemblages (Kautsky et al., 1999). A — transects 1–3, B — transects 4–5, C — transects 6, 9, D — transects 8, 10, E — transect 7. Values in bold indicate significant difference at p<0.05

<table>
<thead>
<tr>
<th>Region</th>
<th>A</th>
<th>B</th>
<th>C</th>
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<tr>
<td>Abundance</td>
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</tr>
<tr>
<td>B</td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
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<tr>
<td>D</td>
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<td>0.02</td>
<td>0.64</td>
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<td>E</td>
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<td>0.01</td>
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<td>Biomass</td>
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<td>B</td>
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<td>C</td>
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<td>D</td>
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<td>0.03</td>
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Figure 1. Study area. Numbers indicate the location of the transects. The left bar shows average biomass, the right bar average abundance of macrozoobenthos in the transect.
Figure 2. Average abundance and biomass values of different taxonomic groups of macrofauna with 95% confidence intervals in shallow water vascular plant communities (n=18) (A), shallow (< 1 m) unvegetated sandy bottoms at the south-eastern (n=9) (B) and north-western coast (n=12) (C), unvegetated sand and gravel bottoms at 1–4 m depth (n=27) (D), unvegetated sand and gravel bottoms at 5–6 m depth (n=8) (E) and hard bottom types (boulders or limestone) with algal vegetation (n=20) (F).
Figure 3. The proportion of different trophic groups in terms of abundance and biomass at different transects.
Figure 4. The proportion of marine, brackish and fresh-water species in terms of abundance and biomass at different transects.
Figure 5. MDS ordination of sampling sites based on macrozoobenthos log-transformed abundance. On the ordination of study sites the number of transects, depth, salinity, bottom type, dominant plant species and type of plant communities are extrapolated. Bottom types are: 1 — stone, 2 — sandy gravel, 3 — gravelly sand, 4 — sand, 5 — gravel clay, 6 — clay sand, 7 — clay. Dominant plant species are: 1 — no vegetation, 2 — Cladophora glomerata Kütz., 3 — Cladophora rupestris Kütz., 4 — Fucus vesiculosus L., 5 — Furcellaria lumbricalis J. V. Lamour, 6 — Myriophyllum spicatum L., 7 — Potamogeton pectinatus L., 8 — Zannichelia palustris L. Different types of plant communities (according to Kautsky et al., 1999) characterize different transects: A — transects 1–3; B — transects 4, 5; C — transects 6, 9; D — transects 8, 10; E — transect 7.
Figure 6. MDS ordination of sampling sites based on macrozoobenthos log-transformed biomass. For further explanation see Fig. 5.
Figure 7. Average abundances and biomasses of macrozoobenthos on different sediment types in the coastal sea of the Gulf of Riga in the 1960s (Järvekülg, 1979) and in 1995–96. Confidence intervals are shown for 1995–96.
CHANGES IN ZOOPLANKTON COMMUNITIES IN ESTONIAN WATERS BETWEEN THE 1970S AND 1990S. AN EXAMPLE FROM THE NORTHERN COAST OF SAAREMAA AND MUGA BAY

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Abstract: The composition of Munga Bay and the coastal area of Saaremaa Island water bodies has changed over the past 30 years. The area has been subject to sewage effluent discharges and increased industrial activities. Changes in the water bodies have led to changes in the structure and composition of the zooplankton communities. The aim of this study was to assess the changes in the composition of zooplankton communities in Munga Bay and the coastal area of Saaremaa Island over the past 30 years. The results show that the changes in the zooplankton community structure have been influenced by increased industrial activities and sewage effluent discharges.
CHANGES IN ZOOBENTHIC COMMUNITIES IN ESTONIAN WATERS BETWEEN THE 1970’S AND 1990’S. AN EXAMPLE FROM THE SOUTHERN COAST OF SAAREMAA AND MUUGA BAY

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Abstract. The communities of Muuga Bay and the coastal sea of Saaremaa Island have overcome great changes in last 20 years. Muuga Bay was influenced by Maardu Chemical Plant and large-scale dredging works. Coastal area of Saaremaa Island is one of the less polluted regions in Estonian waters. In Muuga Bay, dredging seems to have "buffered" the impact of Maardu Chemical Plant which has resulted in an increase of species diversity and abundance values of macrozoobenthos. After closing of the plant many new species have recolonized this study area. In the coastal sea of Saaremaa no new species have been found in last 20 years. The number of species has significantly diminished (among them several phytophilous species).

Key words: zoobenthos, Gulf of Finland, Gulf of Riga, long-term changes

Introduction

Several studies have been carried out to evaluate the impact of pollution upon macrozoobenthos in Estonian coastal sea (Järvekülg, 1969; Järvekülg & Seire, 1985; Kotta & Kotta, 1995). Still no papers are available concerning the long-term development of the zoobenthic communities situated in unpolluted areas as well as in the areas where the amount of sewage effluents have been considerably reduced.

Hence, in this paper we compare the changes which occurred at the littoral zone of Saaremaa Island with those of Muuga Bay in last 20 years. Saaremaa Island was not influenced by any large-scale pollution, whereas the development of macrozoobenthos in Muuga Bay was inhibited by Maardu Chemical Plant till the early 1990’s (shut-down of the plant).
Material and Methods

Study area. Studies were carried out in the southern part of the coastal sea of Saaremaa Island in 1972–73, 1990 and 1993 and in Muuga Bay in 1975–78, 1980–83 and 1991–94 (fig. 1).

Figure 1. Study area; x, ◆, ○, - sampling stations; ◆-dredging areas; ○ - accumulation areas; ○, ○-open areas; ◆-closed areas.
The coastal sea of Saaremaa Island is considered as one of the less polluted areas of Estonian waters. Our study area covers (moving from west to east) Kasti Bay, Sutu Bay, Kõiguste Bay, Tepu Bay and Unguma Bay. Total number of stations was 47. Depth ranged from 0.5 to 10 m, most stations occurred between 1 and 5 m. Depending on water exchange between the Gulf of Riga and the Baltic Proper, the salinity ranges from 6% to 7%, rarely to 8% in the area studied. Dominant bottom types were gravel, sand and mud bottoms which occurred almost in equal proportions. We distinguished a mixed type of gravel and sand bottom which had developed into sand bottom type in last 20 years (see accumulation areas in Fig. 1). Low-scale dredging works were carried out on mud bottoms in Kõiguste Bay in 1990 (dredging areas in Fig. 1).

During last decades human activities had played a major role in the development of the macrozoobenthic communities in Muuga Bay. As a major source of pollution, Maardu Chemical Plant enriched seawater with phosphorus. Data about the sewage input was never published. Sampling was performed at 5, 10, 20, 30, 50 and 70 m depth along a transect. Nearly each depth level has a different sediment type. Starting from the shallower areas these are sand, mud sand, mud, mud clay, clay and mud bottoms. Salinity values are similar to those of Saaremaa study area. Tremendous changes were expected when large-scale dredging works were performed in the 1980’s (see dredging areas in Fig. 1) and Maardu Chemical Plant was closed in early 1990’s.

**Sampling procedure.** Samples were collected yearly in late summer. A Van Veen bottom grab (0.1015 m², 25 kg) was used for sampling in Muuga Bay and a modified Petersen bottom grab (0.0172 m², 10 kg) in the coastal sea of Saaremaa. Bottom dredge was additionally used when gravel bottoms or abundant sea-vegetation occurred.

Sediments were washed through a 0.25 mm mesh and the samples were preserved in 4 % buffered formaldehyde solution. In the laboratory, animals were counted under stereo dissecting microscope. Total wet weights for each taxa were found to the nearest 0.5 mg.

**Statistical analysis.** Statistical analysis was performed using “Statistica”. A significance level of 0.05 was adopted for all statistical tests. After testing for normality of the data (Kolmogorov-Smirnov test for goodness of fit) and homogeneity of variance (Bartlett’s, Hartley’s tests), the analysis of variance (Sokal & Rohlf, 1981) was performed on the values of biomass, abundance and species number of macrozoobenthos. The sediment type, bay and year were involved as factors, the depth as covariate.

**Results**

**Coastal sea of Saaremaa.** Anova showed (Table 1) that site was highly significant in describing the biomass, abundance and species number of macrozoobenthos in the coastal sea of Saaremaa. There were significant
differences in species number between the two periods of study as well as between sediment types. Number of species differed between depths ($R = -0.27$, $p = 0.0101$).

Table 1

<table>
<thead>
<tr>
<th>Model</th>
<th>Factor</th>
<th>Interaction</th>
<th>Covariate</th>
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</thead>
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<td>1. Biomass</td>
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<tr>
<td>2. Abundance</td>
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<td>3. Sp. number</td>
<td>Interaction</td>
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<td>4. Biomass</td>
<td>Study site</td>
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<td>5. Abundance</td>
<td>Interaction</td>
<td>0.3197</td>
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<tr>
<td>6. Sp. number</td>
<td>Depth</td>
<td>0.0000</td>
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</tr>
</tbody>
</table>

Total biomass and abundance have not significantly changed during last 20 years. These values were 90.1 g*m$^{-2}$ and 4553 ind*m$^{-2}$ in 1972 and 73.2 g*m$^{-2}$ and 1953 ind*m$^{-2}$ in 1993.

The number of species per station has diminished for all sediment types (Fig. 2). As an exception no changes in species number has been recorded at dredging areas. The mean value was 4.3±0.8 species per station in both periods. In 1972 the species number at the area of sand accumulation significantly exceeded ($p = 0.0128$) the species number of both sand and gravel bottoms. In 1993 this difference was less marked ($p = 0.0838$).

![Figure 2](image-url)
The number of species is higher on the sediments with coarser particles. There is a significant difference in species number between mud and other sediments in both periods (p < 0.001 in 1972 and p = 0.0285 in 1993).

The following species recorded in 1972 were missing at the sediment types studied in 1993: *Idothea viridis* (Slabber), *Asellus aquaticus* (L.) Racovitza, *Jaera albifrons* Leach, *Lymnea peregra* (O.F. Müll.), *Oligochaeta* spp., *Trichoptera* larvae and *Coleoptera* larvae. *Hirudinea* spp., *Saduria entomon* (L.) and *Odonata* larvae have dissappeared at gravel bottoms; *Hirudinea* spp., *Monoporeia affinis* Lindström, *S. entomon*, *Chironomidae larvae*, *Diptera* larvae, *Mya arenaria* L. and *Bithynia tentaculata* (L.) at sand bottoms; *Potamopyrgus jenkinsi* (Smith) at mud bottoms; *Chironomidae larvae* at the bottoms of sand accumulation and *Chironomidae larvae*, *Diptera larvae* and *Lymnea stagnalis* (L.) in the dredged area.

*Macoma balthica* (L.), *Cerastoderma lamarcki* (Reeve) comprised more than 10 % (sometimes over 75 %) of the total abundance and biomass of macrozoobenthic community at most stations in 1993. The mean values were correspondingly 512 ind*m^-2^ and 29.2 g*m^-2^ for *Macoma* and 323 ind*m^-2^ and 14.8 g*m^-2^ for *Cerastoderma*.

A comparison of the biomasses, abundances and species numbers between the study sites indicated the following. Kõiguste Bay may be divided into two functionally different parts: open and closed areas (see Fig. 1). As compared to other study sites the biomass of macrozoobenthos was considerably higher in the open part of Kõiguste Bay and Kasti Bay and higher abundances were found in Kasti Bay and the open and closed parts of Kõiguste Bay (Fig.3). For the most study sites the number of species significantly decreased in last 20 years. Only at Tepu Bay this trend was not observed. The structure of community differed in the open and closed parts of Kõiguste Bay . *B. tentaculata* had higher biomass and abundance values in closed sea-areas and *Theodoxus fluviatilis* (L.) had higher biomass and abundance values in open sea-areas in 1972. These differences were not found in 1993. During the last 20 years only 3 bivalve species (*M. balthica*, *M. arenaria*, *B. tentaculata*) have increased their biomass and abundance values in open sea-areas. In closed sea-areas the values of abundance have decreased in last 20 years.

**Muuga Bay.** Despite the fact that Muuga Bay is relatively open and exposed to currents, no macrobenthic life was detected at the 5 m depth in 1975. Very low biomass and abundance values were found at the depths between 10 and 30 m (mean values less than 1 g*m^-2^ and 1 ind*m^-2^). The characteristical species were *Nereis diversicolor* (O.F. Müll.), *Oligochaeta* spp. and *Chironomidae larvae*.

In the beginning of the 80's very dense populations of four species – *M. balthica*, *N. diversicolor*, *M. edulis* L. and *M. arenaria* – were recorded at 5–30 m depths. High abundances were observed only in a period of one year. The peak of abundance of *M. balthica* had a time-lag of one or two years at deeper stations as compared to the shallower areas. In the beginning of the 90's even
higher values of abundance and biomass were recorded at 5–30 m depths as compared to the maxima in the 80’s. Fig. 4 represents the changes in biomass of *M. edulis*, *M. arenaria*, *M. balthica* and *N. diversicolor* in the study area during the last 20 years. New immigrants recorded in the shallower part of the study area in last 10 years were *Harmothoe sarsi* (Malmgren), *Corophium volutator* (Pall.), *Gammarus salinus* Spooner, *P. affinis* and *Hydrobia spp.*

Figure 3. Mean values of biomass, abundance and species number of macrozoobenthos with 95% confidence intervals in the coastal sea of Saaremaa in 1972 and 1993.
Figure 4. Biomass of *Mytilus edulis*, *Mya arenaria*, *Macoma balthica* and *Nereis diversicolor* in Muuga Bay in 1975–1994.
Typical species in deeper areas (50–70 m) were *Halicryptus spinulosus* (v. Siebold), *H. sarsi*, *Pontoporeia femorata* Kröyer, *M. affinis*, *S. entomon* and *M. balthica*. Their abundance and biomass did not vary greatly in 1975–93. Fig. 5 depicts the biomass distribution by depths in 1975–78, 1980–83 and 1991–94. In the mid-70's the dense macrobenthic communities were found only at 50–70 m depths. However, after the 70's the total biomass has increased about 10 times at 5–30 m depths.

![Graph](image)

**Figure 5.** The relationship between the depth and biomass of macrozoobenthos in Muuga Bay during the three periods of investigation (95% confidence intervals are shown).

**Discussion**

The structure of macrozoobenthic communities has changed greatly both in the coastal sea of Saaremaa and Muuga Bay in last 20 years. Though, two communities totally differ in their development.

The coastal sea of Saaremaa had relatively high number of species in the 1970's. In the 1990's the bulk of the species have dissappeared (or have low biomass and abundance values). Among them *I. viridis*, *A. aquaticus*, *J. albifrons* and *L. peregra*, considered as phytophilous species (Järvekülg, 1979), were missing on all bottom sediments in the 1990's. The decrease in species number is thought to be connected to the poorer transparency of water, consequently reducing the growth of algae (Kukk, 1993). Algae, in turn, made possible the occurrence of numerous species of crustaceans and molluscs in the 1970's.

In both periods a relatively high number of species were found at the areas of sand accumulation. Probably, patchiness of the spatial distribution of two...
different sediment types (gravel and sand) in the area of sand accumulation enables to support a more diverse and abundant community.

The bottom relief of Kõiguste and Kasti Bays are similar. Both bays are open and have a steep slope towards the Gulf of Riga which facilitates the water exchange between the Gulf of Riga and these bays. Other bays are surrounded by large shallower sea-areas. Hence, water regime might be a factor influencing biomass, abundance and species composition of a macrozoobenthic community.

The second part of the study area, Muuga Bay, encountered a strong stress due to Maardu Chemical Plant till the 1990's. The southern part of Muuga Bay was completely defaunated in 1960 (Järvekülg, 1969). In 1975–78 very low species diversity was recorded in this area.

Another crucial factor influencing the development of macrozoobenthos of the bay was dredging works in 7–15 m depths mainly during 1980–82. Dredged sediments were transported to the shallower area. This shallow region, previously defaunated by Maardu Chemical Plant, became land.

Dredging resulted in the increase of the small particles in the sea-water. Although a very high concentration of particles is thought to inhibit the growth of suspension-feeders (Bricelj et al., 1984; Murphy, 1985; Grizzle & Lutz, 1989) an increase in the abundance of two suspension-feeders *M. edulis* and *M. arenaria* as well as of a facultative filter-feeder *N. diversicolor* (Riisgård, 1991) was observed in the shallower study area in the beginning of the 80’s. The peak of the abundance of *M. balthica* had a time-lag of one year at deeper stations as compared to the abundances of suspension feeders in the shallower area. It indicates that dredging works directly increased the densities of suspension-feeders. Spreading of organic particles later positively influenced *M. balthica*, which is primarily a deposit-feeder (Hummel, 1985). Similarly Poiner and Kennedy (1984) found that dredging increased the species richness and total abundance in adjacent benthic areas.

Second increase in the densities of *M. balthica* in the 1990’s may be attributed to the closing of the Plant. The increase of species diversity in last 10 years reflects the improved ecological conditions of the bay.

As a conclusion, the communities of the coastal sea of Saaremaa are still more diverse than these of Muuga Bay. But a trend towards increased similarity of the communities is observed.

References


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