DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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IMPACT OF EUTROPHICATION AND BIOLOGICAL INVASIONS ON THE STRUCTURE AND FUNCTIONS OF BENTHIC MACROFAUNA

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PRESS

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LIST OF ORIGINAL PUBLICATIONS

I. 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*).

II. 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)

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).

IV. Kotta, J., Kotta, I. & Viitasalo, I. 2000. Effect of diffuse and point source nutrient supply on the low diverse macrozoobenthic communities of the northern Baltic Sea. *Boreal Environ. Res*. (in press)

V. Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I. & Lumberg, A. 1999. Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. *ICES J. Mar. Sci.*, **56** Suppl., 33–40.

VI. Kotta, J. & Orav, H. Factors affecting the distribution, abundance and biomass of invertebrate fauna in the Väinameri (north-eastern Baltic Sea) (submitted to *Ann. Zool. Fenn.*).

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

VIII. Kotta, I. & Kotta, J. 1997. 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. In *Proc. 14th Baltic Mar. Biol. Symp.* (Ojaveer, E., ed.). Estonian Academy Publishers, Tallinn, 70–79.

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 lubricalis* 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 Ponto-Caspian 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 outcompete 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.

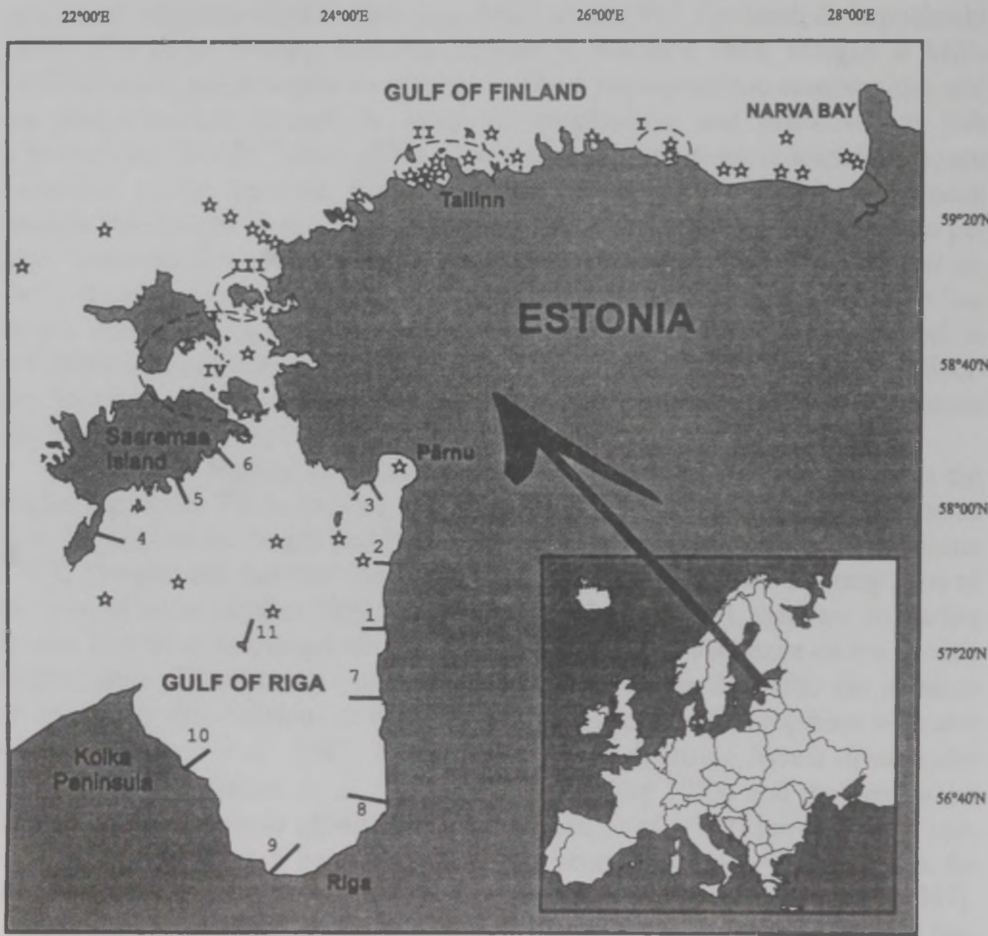

Figure 1. Sampling stations. Dashed circles indicate sampling areas: I, Kunda Bay (15 stations); II, Tallinn and Muuga bays (40 stations); III, coastal sea off Vormsi Island (15 stations); IV, Väinameri Archipelago (90 stations). Stars represent the stations of the Estonian Coastal Monitoring Programme, 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 & Mihnea 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 m^2. 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 (Kiørboe *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 μg 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-indigeneous 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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REFERENCES

Aarnio, K., Bonsdorff, E. & Rosenback, N. 1996. Food and feeding habits of juvenile flounder *Platichtys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Åland Archipelago, northern Baltic Sea. *J. Sea Res.*, **36**, 311–320.

Aneer, G. 1975. Composition of food of the Baltic herring (*Clupea harengus* v *membras* L.), fourhorn sculpin (*Myoxocephalus quadricornis* L.) and eel-pout (*Zoarces viviparus* L.) from deep soft bottom trawling in the Askö-Landsort area during two consecutive years. *Merentutkimuslait. Julk.*, **239**, 146–154.

Atkins, S. M., Jones, A. M. & Garwood, P. R. 1987. The ecology and reproductive cycle of a population of *Marenzelleria viridis* (Annelida: Polychaeta: Spionidae) in the Tay Estuary. *Proc. R. Soc. Edinburgh*, **92**B, 311–322.

Baker, H. & Stebbins, G. 1965. *The Genetics of Colonizing Species*. Academic Press, New York.

Barnes, R. S. K. & Hughes, R. N. 1988. *An Introduction to Marine Ecology*. Blackwell Scientific Publications, Oxford.

Bayne, B. L., Hawkins, A. J. S., Navarro, E. & Iglesias, I. P. 1989. Effects of seston concentration on feeding digestion and growth in the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.*, **55**, 47–54.

Bick, A. & Burckhardt, R. 1989. Erstnahweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum. *Mitt. Zool. Mus. Berl.*, **65**, 237–247.

Bonsdorff, E., Blomqvist, E. M., Mattila, J. & Norkko, A. 1997a. Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuar. Coast. Shelf Sci.*, **44** (Suppl. A), 63–72.

Bonsdorff, E., Blomqvist, E. M., Mattila, J. & Norkko, A. 1997b. Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanol. Acta*, **20**, 319–328.

Bonsdorff, E. & Pearson, T. H. 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional group approach. *Aust. J. Ecol.*, **24**, 312–326.

Branch, G. M. 1984. Competition between marine organisms: ecological and evolutionary implications. *Oceanogr. Mar. Biol. Annu. Rev.*, **22**, 429–593.

Brawley, S. H. & Adey, W. H. 1981. Micrograzers may affect macroalgal density. *Nature*, **292**, 177.

Carlton, J. T. 1996. Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.*, **78**, 97–106.

Carlton, J. T. & Geller, J. B. 1993. Ecological roulette: the global transport of nonindigeneous marine organisms. *Science (Wash.)*, **261**, 78–82.

Cederwall, H. 1977. Annual macrofauna production of a soft bottom in the northern Baltic Proper. In *Biology of Benthic Organisms. Proc. 11th Europ. Mar. Biol. Symp.* (Keegan, B. F., Ceidigh, P. O. & Boaden, P. J. S., eds.). Pergamon Press, Oxford, 155–164.

Clarke, K. R. & Warwick, R. M. 1994. *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, Plymouth.

Cloern, J. E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.*, **9**, 191–202.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Cranford, P. J. & Hargrave, B. T. 1994. In situ time-series measurement of ingestion and absorption rates of suspension-feeding bivalves: *Pelacopecten magellanius*. *Limnol. Oceanogr.*, **39**, 730–738.

Daehler, C. C. & Strong, D. R. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biol. Conserv.*, **78**, 51–58.

Edgar, G. J. 1983. The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. *J. Exp. Mar. Biol. Ecol.*, **70**, 205–255.

Ejdung, G. 1998. Behavioural responses to chemical cues of predation risk in a three-link Baltic Sea food chain. *Mar. Ecol. Prog. Ser.*, **165**, 137–144.

Essink, K. & Kleef, H. L. 1993. Distribution and life cycle of the north American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. *Neth. J. Aq. Ecol.*, **27**, 237–246.

George, J. D. 1966. Reproduction and early development of the spionid polychaete, *Scolecolepides viridis* (Verrill). *Biol. Bull.*, **130**, 76–93.

Gollasch, S. & Leppäkoski, E (eds.). 1999. *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*. Nordic Council of Ministers, Copenhagen.

Gollasch, S., Minchin, D., Rosenthal, H. & Voigt, M (eds.). 1999. *Exotics Across the Ocean Case Histories on Introduced Species*. Department of Fishery Biology, Institut for Marine Science, University of Kiel, Germany.

Gray, J. S. 1992. Eutrophication in the sea. In *Marine Eutrophication and Population Dynamics. Proc. 25th Eur. Mar. Biol. Symp.* (Columbo, G. C., Ferrari, I., Ceccherelli, V. U. & Rossi, R., eds.). Olsen & Olsen, Fredensborg, 3–15.

Gruszka, P. 1999. The River Odra estuary as a gateway for alien species immigration to the Baltic Sea basin. *Acta Hydrochim. Hydrobiol.*, **27**, 374–382.

Haahtela, I. 1990. What do Baltic studies tell us about the isopod *Saduria entomon* (L.)? *Ann. Zool. Fenn.*, **27**, 269–278.

Hällfors, G., Niemi, Å., Ackefors, H., Lassig, J. & Leppäkoski, E. 1981. Biological oceanography. In *The Baltic Sea* (Voipio, A., ed.). Elsevier Oceanography Series, Amsterdam, **30**, 219–274.

Hawkins, S. J. & Hartnoll, R. G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.*, **21**, 195–282.

HELCOM, 1997. Third periodic assessment of the state of the marine environment in the Baltic Sea, 1989–1993. *Balt. Sea Environ. Proc.*, **64B**, 1–252.

Herman, P. M. J. & Scholten, H. 1990. Can suspension-feeders stabilize estuarine ecosystems? In *Trophic Relationships in the Marine Environment. Proc. 24th Eur. Mar. Biol. Symp.* (Barnes, M. & Gibson, R. N., eds.). Aberdeen University Press, Aberdeen, 104–116.

Hill, C. 1992. Interactions between year classes in the benthic amphipod *Monoporeia affinis*: effects on juvenile survival and growth. *Oecologia*, **91**, 157–162.

Hill, C. & Elmgren, R. 1992. Predation by the isopod *Saduria entomon* on the amphipods *Monoporeia affinis* and *Pontoporeia femorata*: experiments on prey vulnerability. *Oecologia*, **91**, 153–156.

Hiscock, K. & Hoare, R. 1973. A portable suction sampler for rock epibiota. *Helgoländer Meeresunters.*, **25**, 35–38.

Holmlund, M. B., Peterson, C. H. & Hay, M. E. 1990. Does algal morphology affect amphipod susceptibility to fish predation? *J. Exp. Mar. Biol. Ecol.*, **139**, 65–83.

Horgan, M. J. & Mills, E. L. 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. *Can. J. Fish. Aquat. Sci.*, **54**, 249–255.

Hull, S. C. 1987. Macroalgal mats and species abundance: a field experiment. *Estuar. Coast. Shelf Sci.*, **25**, 519–532.

Jansson, A. M. 1974. Community structure, modelling and simulation of the *Cladophora* ecosystem in the Baltic Sea. *Contrib. Askö Lab. Univ. Stockholm*, **5**, 1–130.

Jansson, A. M., Kautsky, N., von Oertzen, J. A., Schramm, W., Sjöstedt, B., von Wachenfelddt, T. & Wallentinus, I. 1982. Structural and functional relationships in a southern Baltic *Fucus* ecosystem – a joint study by the BMB Phytobenthos Group. *Contrib. Askö Lab. Univ. Stockholm*, **28**, 1–95.

Jansson, K. 1994. *Alien Species in the Marine Environment. Introductions to the Baltic Sea and the Swedish West Coast.* Report 4357. Swedish Environmental Protection Agency, Solna.

Järvekülg, A. 1979. *Benthic Fauna of the Eastern Baltic Sea.* Valgus, Tallinn (in Russian).

Jonsson, P. & Carman, R. 1994. Changes in deposition of organic matter and nutrients in the Baltic Sea during the twentieth century. *Mar. Pollut. Bull.*, **28**, 417–426.

Jørgensen, C. B., Larsen, P. S. & Riisgård, H. U. 1990. Effects of temperature on the mussel pump. *Mar. Ecol. Prog. Ser.*, **64**, 89–97.

Kangas, P. 1972. Quantitative sampling equipment for the littoral benthos. II. *IBP i Norden*, **10**, 9–16.

Kangas, P., Autio, H., Hällfors, G., Luther, A., Niemi, Å. & Salemaa, H. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–1981. *Acta Bot. Fenn.*, **118**, 1–27.

Kautsky, H. 1995. Quantitative distribution of sublittoral plant and animal communities along the Baltic Sea gradient. In *Biology and Ecology of Shallow Coastal Waters. Proc. 28th Eur. Mar. Biol. Symp.* (Eleftheriou, A., Ansell, A. D. & Smith, C. J., eds.). Olsen & Olsen, Fredensborg, 23–30.

Kautsky, H., Kautsky, L., Kautsky, N., Kautsky, U. & Lindblad, C. 1992. Studies on the *Fucus vesiculosus* community in the Baltic Sea. *Acta Phytogeogr. Suec.*, **78**, 33–49.

Kautsky, H., Martin, G., Mäkinen, A., Borgiel, M., Vahteri, P. & Rissanen, J. 1999. Structure of phytobenthic and associated animal communities in the Gulf of Riga. *Hydrobiologia*, **393**, 191–200.

Kautsky, N. & Evans, S. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.*, **38**, 201–212.

Kautsky, U. 1995. *Ecosystem Processes in Coastal Areas of the Baltic Sea.* Doctoral dissertation, Stockholm University, Sweden.

Kiørboe, T., Møhlenberg, F. & Nøhr, O. 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia*, **19**, 193–205.

Kolbe, K., Kaminski, E., Michaelis, H., Obert, B. & Rahmel, J. 1995. Macroalgal mass development in the Wadden Sea: first experiences with a monitoring system. *Helgol. Meeresunters.*, **49**, 1–4.

Kotta, J. 2000. First record of the talitrid amphipod *Orchestia cavimana* in the northern Baltic Sea. *Proc. Est. Acad. Sci. Biol. Ecol.*, **49**, 221–224.

Kotta, J. & Kotta, I. 1995. The state of macrozoobenthos of Pärnu Bay in 1991 as compared to 1959–60. *Proc. Est. Acad. Sci. Ecol.*, **5**, 26–37.

Kotta, J. & Kotta, I. 1998. Distribution and invasion ecology of *Marenzelleria viridis* in the Estonian coastal waters. *Proc. Est. Acad. Sci. Biol. Ecol.*, **47**, 212–220.

Kotta, J., Kotta, I. & Kask, J. 1999. Benthic animal communities of exposed bays in the western Gulf of Finland (Baltic Sea). *Proc. Est. Acad. Sci. Biol. Ecol.*, **48**, 107–116.

Kotta, J., Kotta, I., Martin, G. & Kukk, H. 1998a. A survey of data published on the littoral zoobenthos of the Gulf of Riga. *Proc. Est. Acad. Sci. Biol. Ecol.*, **47**, 83–97.

Kotta, J., Orav, H. & Kotta, I. 1998b. Distribution and filtration activity of the zebra mussel, *Dreissena polymorpha*, in the Gulf of Riga and the Gulf of Finland. *Proc. Est. Acad. Sci. Biol. Ecol.*, **47**, 32–41.

Kryger, J. & Riisgård, H. U. 1988. Filtration rate capacities in 6 species of European freshwater bivalves. *Oecologia*, **77**, 34–38.

Kube, J., Gosselck, F. & Powilleit, M. 1997. Long-term changes in the benthic communities in the Pomeranian Bay (southern Baltic Sea). *Helgol. Meeresunters.*, **51**, 399–416.

Kullenberg, G. 1981. Physical oceanography. In *The Baltic Sea* (Voipio, A., ed.). Elsevier Oceanography Series, Amsterdam, **30**, 135–181.

Lagzdins, G. & Pallo, P. 1994. *Marenzelleria viridis* (Verrill) (Polychaeta, Spionidae) – a new species for the Gulf of Riga. *Proc. Est. Acad. Sci. Biol.*, **43**, 184–188.

Laine, A., Sandler, A. O., Andersin, A.-B. & Stigzelius, J. 1997. Long-term changes of macrozoobenthos in the eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. *J. Sea Res.*, **38**, 135–159.

Leppäkoski, E. 1991. Introduced species – resource or threat in brackish water seas? Examples from the Baltic and the Black Sea. *Mar. Pollut. Bull.*, **23**, 219–223.

Leppäkoski, E. & Bonsdorff, E. 1989. Ecosystem variability and gradients. Examples from the Baltic Sea as a background for hazard assessment. In *Chemicals in the Aquatic Environment. Advanced Hazard Assessment* (Landner, L., ed.). Springer Verlag, Berlin, 6–58.

Leppäkoski, E. & Mihnea, P. E. 1996. Enclosed seas under man-induced change: a comparison between the Baltic and Black Seas. *Ambio*, **25**, 380–389.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. *Am. Nat.*, **112**, 23–39.

Lubchenco, J. 1982. Effects of grazers and algal competitors on fucoid colonization in tide pools. *J. Phycol.*, **18**, 544–550.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology*, **64**, 1116–1123.

Lubchenco, J. & Menge, B. A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, **59**, 67–94.

Malm, T. 1999. *Distribution patterns and ecology of Fucus serratus L. and Fucus vesiculosus L. in the Baltic Sea.* Doctoral dissertation, University of Stockholm, Sweden.

Mardiste, H., 1970. Väinameri. In *Lääne-Eesti rannikualade loodus* (Kumari, E., ed). Valgus, Tallinn, 7–16.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.*, **46**, 355–496.

McKnight, B. N., Garton, D. W., Berg, D. J., Stoeckmann, A. M. & Haag, W. R. 1993. Biology of recent invertebrate invading species in the Great Lakes: the spiny water flea, *Bythotrephes cederstroemi*, and the zebra mussel, *Dreissena polymorpha*. In *Biological Pollution: the Control and Impact of Invasive Exotic Species* (McKnight, B. N., ed.). Indiana Academy of Science, Indianapolis, 63–84.

Mills, E. L., Leach, J. H., Carlton, J. T. & Secor, C. L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.*, **19**, 1–54.

Møhlenberg, F. 1995. Regulating mechanisms of phytoplankton growth and biomass in a shallow estuary. *Ophelia*, **42**, 239–256.

Morton, B. 1969. Studies on the biology of *Dreissena polymorpha* Pall. II. Population dynamics. *Proc. Malacol. Soc. Lond.*, **38**, 471–482.

Norkko, A. & Bonsdorff, E. 1996a. Population responses of coastal zoobenthos to stress induced by drifting algal mats. *Mar. Ecol. Prog. Ser.*, **140**, 141–151.

Norkko, A. & Bonsdorff, E. 1996b. Rapid zoobenthic community responses to accumulations of drifting algae. *Mar. Ecol. Prog. Ser.*, **131**, 143–157.

Norkko, A., Bonsdorff, E. & Boström, C. 1993. Observations of the polychaete *Marenzelleria viridis* (Verril) on a shallow sandy bottom on the South coast of Finland. *Mem. Soc. Fauna Flora Fenn.*, **69**, 112–113.

Officer, C. B., Smayda, T. J. & Mann, R. 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.*, **9**, 203–210.

Olenin, S. & Leppäkoski, E. 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. *Hydrobiologia*, **393**, 233–243.

Orav, H. & Kotta, J. 2000. Factors affecting the distribution of benthic invertebrates in the phytal zone of the north-eastern Baltic Sea. *Proc. Est. Acad. Sci. Biol. Ecol.*, **49**, 253–269.

Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93–120.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., Von Holle, B., Moyle, P. B., Byers, J. E. & Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**, 3–19.

Pedersen, M. F. & Borum, J. 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar. Ecol. Progr. Ser.*, **142**, 261–272.

Plinski, M. & Florczyk, I. 1984. Changes in the phytobenthos resulting from the eutrophication of the Puck Bay. *Limnologica (Berlin)*, **15**, 325–327.

Reeders, H. H., Bij de Vaate, A. & Slim, F. J. 1989. The filtration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch lakes with reference to biological water quality management. *Freshwat. Biol.*, **22**, 133–141.

Reusch, T. B. H. & Chapman, A. R. O. 1995. Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) beds. *J. Exp. Mar. Biol. Ecol.*, **192**, 257–271.

Riisgård, H. U. 1991. Filtration rate and growth in the Blue Mussel, *Mytilus edulis* Linneaus, 1758: Dependence on algal concentration. *J. Shellfish Res.*, **10**, 29–35.

Riisgård, H. U. & Møhlenberg, F. 1979. An improved automatic recording apparatus for determining the filtration rate of *Mytius edulis* as a function of size and algal concentration. *Mar. Biol.*, **52,** 61–67.

Rosenberg, R. 1985. Eutrophication – the future marine coastal nuisance? *Mar. Pollut. Bull.*, **16**, 227–231.

Rosenberg, R., Elmgren, R., Fleischer, S., Jonsson, P., Persson, G. & Dahlin, H. 1990. Marine eutrophication case studies in Sweden. *Ambio*, **19**, 102–108.

Rosenberg, G. & Ludyanskiy, M. L. 1994. A nomenclatural review of *Dreissena* (*Bivalvia: Dreissenidae*), with identification of the Quagga Mussel as *Dreissena bugensis. Can. J. Fish. Aquat. Sci.*, **51**, 1474–1485.

Ruesink, J. L., Parker, I. M., Groom, M. J. & Kareiva, P. M. 1995. Reducing the risks of nonindigeneous species introductions: guilty until proven innocent. *Bioscience*, **45**, 465–477.

Ruiz, G. M., Fofonoff, P. & Hines, A. H. 1999. Non-indigeneous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnol. Oceanogr.*, **44**, 950–972.

Salemaa, H. 1979. Ecology of *Idotea* spp. (Isopoda) in the northern Baltic. *Ophelia*, **18,** 133–150.

Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idothea* spp. (Isopoda) in the northern Baltic Sea. *Ophelia*, **27**, 1–15.

Salemaa, H. & Hietalahti, V. 1993. *Hemimysis anomala* G. O. Sars (Crustacea: Mysidacea) – immigration of a Pontocaspian mysid into the Baltic Sea. *Ann. Zool. Fenn.*, **30**, 271–276.

Schrenk, A. G. 1848. Übersicht der Land- und Süsswassermollusken Livlands. *Bull. Soc. Imp. Nat. Moscou*, **XXI**.

Schultz, S., Ærtbjerg, G., Behrends, G., Breuel, G., Ciszewski, P., Horstmann, U., Kononen, K., Kostrichkina, E., Leppänen, J. M., Møhlenberg, F., Sandström, O., Viitasalo, M. & Willén, T. 1992. The present state of the Baltic Sea pelagic ecosystem – an assessment. In *Marine Eutrophication and Population Dynamics. Proc. 25th Eur. Mar. Biol. Symp.* (Columbo, G. C., Ferrari, I., Ceccherelli, V. U. & Rossi, R., eds.). Olsen & Olsen, Fredensborg, 35–44.

Segerstråle, S. 1957. Baltic Sea. *Mem. Geol. Soc. Am.*, **67**, 757–800.

Shurin, A. T. 1953. Bottom fauna in the Gulf of Riga. *Tr. Latv. Odteleniya VNIRO*, **1**, 77–113 (in Russian).

Shurin, A. T. 1961. The grouping of bottom fauna in the Gulf of Riga. *Tr. NIIRH SNH Latv. SSR*, **3**, 343–368 (in Russian).

Simberloff, D. 1991. Keystone species and community effects of biological introductions. In *Assessing Ecological Risks of Biotechnology* (Ginzburg, L. R., ed.). Butterworth-Heinemann, Boston, 1–19.

Simberloff, D. & Von Holle, B. 1999. Positive interactions of nonindigeneous species: invasional meltdown? *Biol. Invasions*, **1**, 21–32.

Stanczykowska, A., Lawacz, W. & Mattice, J. 1975. Use of field measurements of consumption and assimilation in evaluation of the role of *Dreissena polymorpha* Pall. in a lake ecosystem. *Pol. Arch. Hydrobiol.*, **22**, 509–520.

Stigzelius, J., Laine, A., Rissanen, J., Andersin, A.-B. & Ilus, E. 1997. The introduction of *Marenzelleria viridis* (Polychaeta, Spionidae) into the Gulf of Finland and the Gulf of Bothnia (northern Baltic Sea). *Ann. Zool. Fenn.*, **34**, 205–212.

Suursaar, Ü., Astok, V. & Otsmann, M. 1998. The front of Väinameri. *Est. Mar. Inst. Rep. Ser.*, **9**, 23–33.

Thienemann, A. 1950. Verbeitungsgeschichte der Süßwassertierwelt Europas. *Die Binnengewässer*, **18**, 1–809.

Turro, A. & Jakobson, I. 1997. Dynamics of pollution from point sources in Tallinn Bay. *Est. Mar. Inst. Rep. Ser.*, **8**, 73–83.

Valovirta, I. & Porkka, M. 1996. The distribution and abundance of *Dreissena polymorpha* (Pallas) in the eastern Gulf of Finland. *Mem. Soc. Fauna Flora Fenn.*, **72**, 63–78.

Vogt, H. & Schramm, W. 1991. Conspicuous decline of *Fucus* in Kiel Bay (western Baltic): what are the causes? *Mar. Ecol. Prog. Ser.*, **69**, 189–194.

Winkler, H. M. & Debus, L. 1997. Is the polychaete *Marenzelleria viridis* an important food item for fish? In *Proc. 13th Baltic Mar. Biol. Symp.* (Andrushaitis, A., ed.). Institute of Aquatic Ecology, University of Latvia, Riga, 147–151.

Winter, J. E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture*, **13**, 1–33.

Winterhalter, B., Flodén, T., Ignatius, H., Axberg, S. & Niemistö, L. 1981. Geology of the Baltic Sea. In *The Baltic Sea* (Voipio, A., ed.). Elsevier Oceanography Series, Amsterdam, **30**, 1–121.

Wu, L. & Culver, D. A. 1991. Zooplankton grazing and phytoplankton abundance – an assessment before and after invasion of *Dreissena polymorpha*. *J. Great Lakes Res.* **17**, 425–436.

Wulff, F., Rahm, L. & Rodriguez-Medina, M. 1994. Long-term and regional variations of nutrients in the Baltic Sea: 1972–1991. *Finnish Mar. Res.*, **262**, 35–50.

Zettler, M. L. 1996. Successful establishment of the spionid polychaete, *Marenzelleria viridis* (Verrill, 1873), in the Darss-Zingst estuary (southern Baltic) and its influence on the indigeneous macrozoobenthos. *Arch. Fish. Mar. Res.*, **43**, 273–284.

Zettler, M. L. 1997. Bibliography on the genus *Marenzelleria* and its geographical distribution, principal topics and nomenclature. *Aquat. Ecol.*, **31**, 233–258.

EUTROFEERUMISE JA BIOLOOGILISTE INVASIOONIDE MÕJU PÕHJALOOMASTIKU KOOLUSTE STRUKTUURILE JA ELUTEGEVUSELE

Kokkuvõte

Põhjaloomastikku uuriti Läänemere kirdeosa rannikumeres. Mitmemõõtmeliste statistiliste analüüside abil hinnati seoseid erinevate keskkonnategurite ja loomakoosluste struktuuri vahel. Põhjataimestik mõjutas kõige enam põhjaeluviisiliste selgrootute kooslusi vähe eutrofeerunud merealadel ning sette tüüp ja toiteelementide hulk eutrofeerunud merealadel. Põhjakoosluste liigiline mitmekesisus oli väiksem eutrofeerunud merealadel. Samas on viimaste aastakümnete jooksul põhjakoosluste struktuur kogu uurimisalal sarnaselt muutunud.

Merekeskkonna eutrofeerumise tagajärjel suureneb märkimisväärselt niitjate vetikate ja filtreerijate karpide hulk rannikumeres. Niitjate vetikate vohamise tagajärjel on ulatuslikel aladel *Fucus vesiculosus*'e varud oluliselt kahanenud. Kõige arvukam põhjaeluviisiline herbivoor, kakandiline *Idotea baltica*, on üle läinud alternatiivsele toidule. *I. baltica* arvukus oli kõrgeim mere madalamates osades, kus niitja vetika *Pilayella littoralis* hulk *Furcellaria lumbricalis* pealiskasvuna oli suurim. Süües kiirekasvulist pealiskasvu, parandavad kakandilised punavetika *F. lumbricalis* kasvutingimusi.

Söödava rannakarbi, *Mytilus edulis*, elutegevuse tagajärjel suunatakse suur osa fütoplanktonist põhjasetetesse. Filtreerimisprotsessi osatähtsus uurimisalal on tõenäoliselt suurim Liivi lahe põhjaosas, mis on tingitud ulatuslike madalate merealade esinemisest ning mõõdukast vee segunemisest. Kevadel tarbis *M. edulis* päevas 1–8% fütoplanktoni varudest ning suvel vastavalt 31–91%. Väiksem *M. edulis*'e mõju mais oli tingitud kõrgest fütoplanktoni biomassist ning külmast mereveest, mis vähendas oluliselt karpide filtreerimiskiirust. Tulemused viitavad sellele, et põhjakooslused kontrollivad sageli pelaagiliste koosluste arengut Läänemere kirdeosa rannikumeres.

Tulnukliikidest mõjutavad kõige enam Läänemere kirdeosa põhjakoosluste arengut Kaspia ja Musta mere vesikonnast pärit rändkarp, *Dreissena polymorpha*, ning Põhja-Ameerika estuaare asustav hulkharjasuss, *Marenzelleria viridis*. *D. polymorpha* asustab peaaegu kogu Liivi lahe rannikumerd ning lisaks ka üksikuid piirkondi Soome lahes. Tänu kõrgele arvukusele mõjutab *D. polymorpha* pelaagiliste ja põhjakoosluste arengut eutrofeerunud merealadel.

M. viridis on asustanud kogu Liivi lahte, Väinamere ning Soome lahe lääne- ja keskosa. *M. viridis*'e levila laieneb aeglaselt Soome lahe idaosa suunas. *M. viridis* populatsioon pole uurimisalal veel stabiliseerunud. Liik on edukalt asustanud nii kõrge troofsusega piirkondi kui ka koosluste poolest võrdlemisi homogeenseid merealasid. *M. viridis* vähendab toidukonkurentsi kaudu kohaliku kirpvähilise *M. affinis* kasvukiirust.

PUBLICATIONS

I

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 (Kiørboe *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 chorophyll *a* equivalent or total chlorophyll (Chl *a* eq) were calculated as Chl a eq = Chl 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 Chl *a* and Pha were measured fluoremetrically (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_{wS} and tot Chl_{wE} are the suspended total chlorophyll content in the aquarium at the start and end of the incubation, respectively, and $\sum$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 *a*, 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 *a* 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 *a* 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 *a* eq and Chl *a*, 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_l) was scaled by shell length, i.e. $G_l = G_{20} \times l^2/20^2$), where G_{20} is the grazing rate of 20 mm individuals and l the shell length (Kiørboe & Møhlenberg 1981).

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 (Kiørboe *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, Kiørboe & 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^{-1} h^{-1}, BSi: 0.89 l^{-1} h^{-1}) that were lower but still comparable to the filtration rate predicted from Kiørboe & 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 prep.), 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

Ansell, A.D. 1974a. Seasonal changes in biochemical composition of the bivalve *Abra alba* from the Clyde Sea area. — Mar. Biol. **25**: 13–20.

Ansell, A.D. 1974b. Seasonal changes in the biochemical composition of the bivalve *Chlamys septenradiata* from the Clyde Sea area. — Mar. Biol. **25**: 85–99.

Asmus, R.M. & H. Asmus 1991. Mussel beds: Limiting or promoting phytoplankton. — J. Exp. Mar. Biol. Ecol. **148**: 215–232

Bayne, B.L., A.J.S. Hawkins, E. Navarro & I.P. Iglesias 1989. Effects of seston concentration on feeding digestion and growth in the mussel *Mytilus edulis*. — Mar. Ecol. Prog. Ser. **55**: 47–54.

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

Cloern, J.E. 1982. Does the benthos control phytoplankton biomass in South Francisco Bay? — Mar. Ecol. Prog. Ser. **9**: 191–202.

Conley, D. & R. Johnston 1995. Biogeochemistry of N, P, and Si in Baltic Sea sediments: Response to a simulated deposition of a spring diatom bloom. — Mar. Ecol. Prog. Ser. **122**: 265–279.

Cranford, P.J. & B.T. Hargrave 1994. In situ time-series measurement of ingestion and absorption rates of suspension-feeding bivalves: *Placopecten magellanius*. — Limnol. Oceanogr. **39**: 730–738.

Foster-Smith, R.L. 1975. The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). — J. Exp. Mar. Biol. Ecol. **17**: 1–22.

Fréchette, M., C.A. Butman & W.R. Geyer 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. — Limnol. Oceanogr. **34**: 19–36.

Hawkins, A.J.S., B.L. Bayne, R.F.C. Mantoura & C.A. Llewellyn 1986. Chlorophyll degradation and absorption throughout the digestive system of the blue mussel *Mytilus edulis* L. — J. Exp. Mar. Biol. Ecol. **96**: 213–223.

Horgan, M.J. & E.L. Mills 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): Implications for freshwater lakes. — Can. J. Fish. Aquat. Sci. **54**: 249–255.

Järvekülg, A. 1979. Benthic fauna of the eastern Baltic Sea. Valgus, pp. 1–372. Tallinn. (in Russian)

Jensen, A. & E. Sakshaug 1970a. Producer-consumer relationships in the sea. I. Preliminary studies on phytoplankton density and *Mytilus* pigmentation. — J. Exp. Mar. Biol. Ecol. **5**: 180–186.

Jensen, A. & E. Sakshaug 1970b. Producer-consumer relationships in the sea. II. Correlation between *Mytilus* pigmentation and the density and composition of phytoplanktonic populations in inshore waters. — J. Exp. Mar. Biol. Ecol. **5**: 246–253.

Jørgensen, C.B., P.S. Larsen & H.U. Riisgård 1990. Effects of temperature on the mussel pump. — Mar. Ecol. Prog. Ser. **64**: 89–97.

Josefson, A.B., J.N. Jensen, T.G. Nielsen & B. Rasmussen 1995. Growth parameters of a benthic suspension feeder along a depth gradient across the pycnocline in the southern Kattegat, Denmark. — Mar. Ecol. Prog. Ser. **125**: 107–115.

Kamermans, P. 1993. Food limitation in cockles (*Cerastoderma edule* (L.)): Influences of location on tidal flat and of nearby presence of mussel beds. — Neth. J. Sea Res. **31**: 71–81.

Kautsky, N. & S. Evans 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. — Mar. Ecol. Prog. Ser. **38**: 201–212.

Kiørboe, T. & F. Møhlenberg 1981. Particle selection in suspension feeding bivalves. — Mar. Ecol. Prog. Ser. **5**: 291–296.

Kiørboe, T., F. Møhlenberg & O. Nøhr 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. — Ophelia **19**: 193–205.

Kotta, I. & J. Kotta 1997. 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. In E. Ojaveer (ed.): Proceedings of the 14th Baltic Marine Biologists Symposium. Estonian Academy Publishers, pp. 70–79. Tallinn, Estonia.

Kotta, J. & I. Kotta 1995. The state of macrozoobenthos of Pärnu Bay as compared to 1959–60. — Proc. Est. Acad. Sci. Ecol. **5**: 26–37.

Kotta, J., I. Kotta, & J. Kask 1999. Benthic animal communities of exposed bays in the western Gulf of Finland (Baltic Sea). — Proc. Est. Acad. Sci. Biol. Ecol. **48**: 107–116.

Loo, L.-O. & R. Rosenberg 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in a eutrophicated marine bay. — J. Exp. Mar. Biol. Ecol. **130**: 253–276.

Mann, R. 1977. An assessment of the use of pigment content as a feeding index in oysters. — Aquaculture **10**: 373–376.

Møhlenberg, F. 1995. Regulating mechanisms of phytoplankton growth and biomass in a shallow estuary. — Ophelia **42**: 239–256.

Møhlenberg, F. & H.U. Riisgård 1978. Efficiency of particle retention in 13 species of suspension-feeding bivalves. — Ophelia **17**: 239–246.

Muschenheim, D.K. & C.R. Newell 1992. Utilisation of seston flux over a mussel bed. — Mar. Ecol. Prog. Ser. **85**: 131–136.

Newell, C.R., S.E. Shumway, T.L. Cucci & R. Selvin 1989. The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. — J. Shellfish Res. **8**: 187–196.

Nichols, F.H. 1984. Increased benthic grazing: One explanation for low phytoplankton biomass in Northern San Francisco Bay during the 1976–1977 drought. — EOS (Trans. Am. Geophys. Un.) **65**: 908.

Officer, C.B., T.J. Smayda & R. Mann 1982. Benthic filter feeding: A natural eutrophication control. — Mar. Ecol. Prog. Ser. **9**: 203–210.

Pastoureaud, A., M. Heral, J. Prou, D. Razet & P. Russu 1996. Particle selection in the oyster *Crassostrea gigas* (Thunberg) studied by pigment HPLC analysis under natural food conditions. — Oceanol. Acta **19**: 79–88

Penry, D.L. & B.W. Frost 1991. Chlorophyll-*a* degradation by *Calanus pacificus*: Dependence on ingestion rate and digestive acclimation to food resources. — Limnol. Oceanogr. **36**: 147–159.

Petersen, J.K. & H.U. Riisgård 1992. Filtration capacity of the ascidian *Ciona intestinalis* and its grazing impact in a shallow fjord. — Mar. Ecol. Prog. Ser. **88**: 9–17.

Peterson, C.H. & R. Black 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. — Estuar. Coast. Shelf Sci. **32**: 405–413.

Redden, A.M., R.J. Thompson & D. Deibel 1993. Effects of short- and long-term freezing of chloropigments in cultured diatoms and bivalve digestive gland and faeces as determined by standard flourometry and HPLC. — Arch. Hydrobiol. **129**: 67–87.

Riisgård, H.U. 1991. Filtration rate and growth in the Blue Mussel, *Mytilus edulis* Linneaus, 1758: Dependence on algal concentration. — J. Shellfish Res. **10**: 29–35.

Riisgård, H. U. & F. Møhlenberg 1979. An improved automatic recording apparatus for determining the filtration rate of *Mytius edulis* as a function of size and algal concentration. — Mar. Biol. **52**: 61–67.

Stålnacke, P., N. Vagstad, T. Tamminen, P. Wassmann, V. Jansons & E. Loigu 1999. Nutrient runoff and transfer from land and rivers to the Gulf of Riga. — Hydrobiologia **410**: 103–110.

Strickland, J.D.H. & T.R. Parsons 1972. A practical handbook of seawater analysis. — Bull. Fish. Res. Bd. Can. **167**: 1–310.

Tamminen, T. & J. Seppälä 1999. Nutrient pools, transformations, ratios and limitation in the Gulf of Riga, the Baltic Sea, during four successional stages. — J. Mar. Syst. **23**: 83–106.

Tande, K. & D. Slagsted 1985. Assimilation efficiency in herbivorous aquatic organisms — The potential of the ratio method using 14C and biogenic silica as markers. — Limnol. Oceanogr. **30**: 1093–1099.

Winter, J.E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. — Aquaculture **13**: 1–33.

Wright, R.T., R.B. Coffin, C.P. Ersing & D. Pearson 1982. Field and laboratory measurements of bivalve filtration of natural bacterioplankton. — Limnol. Oceanogr. **27**: 91–98.

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. $FP_{20} = FP_l * 20^2/l^2$)

Transect	Date	Hours	Depth	Temp.	Salinity	Chl *a*	Chl *a* eq	BSi	Shell length	Sample	Faeces production			
			m	°C	ppt	µg l^{-1}	µg l^{-1}	µg l^{-1}	mm	n	µg Chl *a* eq ind^{-1} h^{-1}		µg BSi ind^{-1} h^{-1}	
						start-end	start-end		range		mean	SD	mean	SD
Kõiguste	9–10 May	16:00–8:00	2	6.1	5.4	16.0–11.3	17.1–15.7		15–21	4	0.202	0.075		
	9–10 May	16:00–8:00	5	6.3	5.5	14.4–13.4	19.1–19.4		13–18	7	0.369	0.225		
	10-May	8:00–21:00	2	5.9	5.5	11.3–9.0	15.7–14.3		16–19	4	0.266	0.082		
	10-May	8:00–21:00	5	5.9	5.5	13.4–8.1	19.4–24.7		13–16	6	0.301	0.144		
	10–11 May	21:00–9:00	2	5.2	5.5	9.0–11.4	14.3–18.6		18	1	0.209			
	10–11 May	21:00–9:00	5	5.3	5.5	8.1–15.3	24.7–21.0		13–16	3	0.294	0.202		
Saulkrasti	13–14 May	21:00–9:00	2	3.6	4.77	35.2–43.5	45.2–62.7		13–15	7	0.228	0.170		
	13–14 May	21:00–9:00	5	3.4	5.20	43.5–50.3	58.9–58.3		16–18	8	0.364	0.114		
	14 May	9:00–21:00	2	5.9	4.92	43.5–71.3	62.7–104.0		13–16	7	0.376	0.361		
	14 May	9:00–21:00	5	5.5	5.05	50.3–60.8	58.3–74.1		16–18	8	0.400	0.106		
Kõiguste	23–24 July	20:00–8:30	2	16.2	5.8	1.2–1.9	3.1–4.1	4.8	23–28	7	0.072	0.025	5.040	0.310
	23–24 July	21:00–9:10	5	15.9	5.7	2.5–2.0	6.5–5.5	7.9	21–24	8	0.160	0.043	7.487	2.770
	24 July	8:30–20:45	2	16.4	5.8	1.9–1.0	4.1–2.6	3.9	24–28	4	0.056	0.013	2.148	0.360
	24–25 July	20:45–7:30	2	16.2	5.7	1.0–1.4	2.6–3.2	3.5	24–28	4	0.037	0.021	2.024	0.964
	25 July	7:30–20:00	2	16.5	5.7	1.4–1.4	3.2–3.5	4.5	24–28	4	0.087	0.022	3.818	0.962
	25–26 July	20:00–8:20	2	16.1	5.7	1.4–1.1	3.5–2.9	4.4	23–26	4	0.103	0.060	3.378	1.676
	25–26 July	20:30–8:45	5	16.2	5.7	1.4–1.6	3.4–4.3	4.5	23–26	4	0.093	0.068	3.275	0.742
	26 July	8:20–20:15	2	16.3	5.7	1.1–1.9	2.9–5.1	5.0	23–25	4	0.128	0.039	3.177	1.343
	26 July	8:45–20:30	5	16.4	5.7	1.6–2.0	4.3–4.8	5.5	23–26	5	0.139	0.054	3.992	1.148

Table 2. Kõiguste transect in July. Slope and intercept of the linear regressions between defaecation rate (Y, μg Chl *a* eq ind^{-1} h^{-1}, μg BSi ind^{-1} h^{-1}) and ambient concentration of food (X, μg Chl *a* l^{-1}, μg Chl *a* eq l^{-1}, μg BSi l^{-1}). For chlorophyll defaecation only the initial linear part of the relation is included (i.e. ambient Chl *a* < 2 μg l^{-1}; ambient Chl *a* eq < 4 μg l^{-1}). The slope of the regression between calculated grazing rate and ambient concentration of chlorophyll is shown in brackets.

Y	X	Slope ± SD, p-level	Intercept ± SD, p-level	R^2
Chl *a* eq defaecation (Chl *a* grazing)	Chla	0.173 ± 0.052, 0.002 (0.446)	–0.177 ± 0.081, 0.04	0.27
Chl *a* eq defaecation (Chl *a* eq grazing)	Chl *a* eq	0.059 ± 0.015, <0.001 (0.152)	–0.127 ± 0.059, 0.04	0.31
BSi defaecation	BSi	0.885 ± 0.145, <0.0001	–0.847 ± 0.830, 0.31	0.52

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.

Transect	Average grazing impact		
	% Chl *a* eq d^{-1}	% Chl *a* d^{-1}	% BSi d^{-1}
Kõiguste (0–5 m)			
May	2.4	3.5	
July	8.5	31.4	96
Saulkrasti (0–9 m)			
May	2.0	2.5	

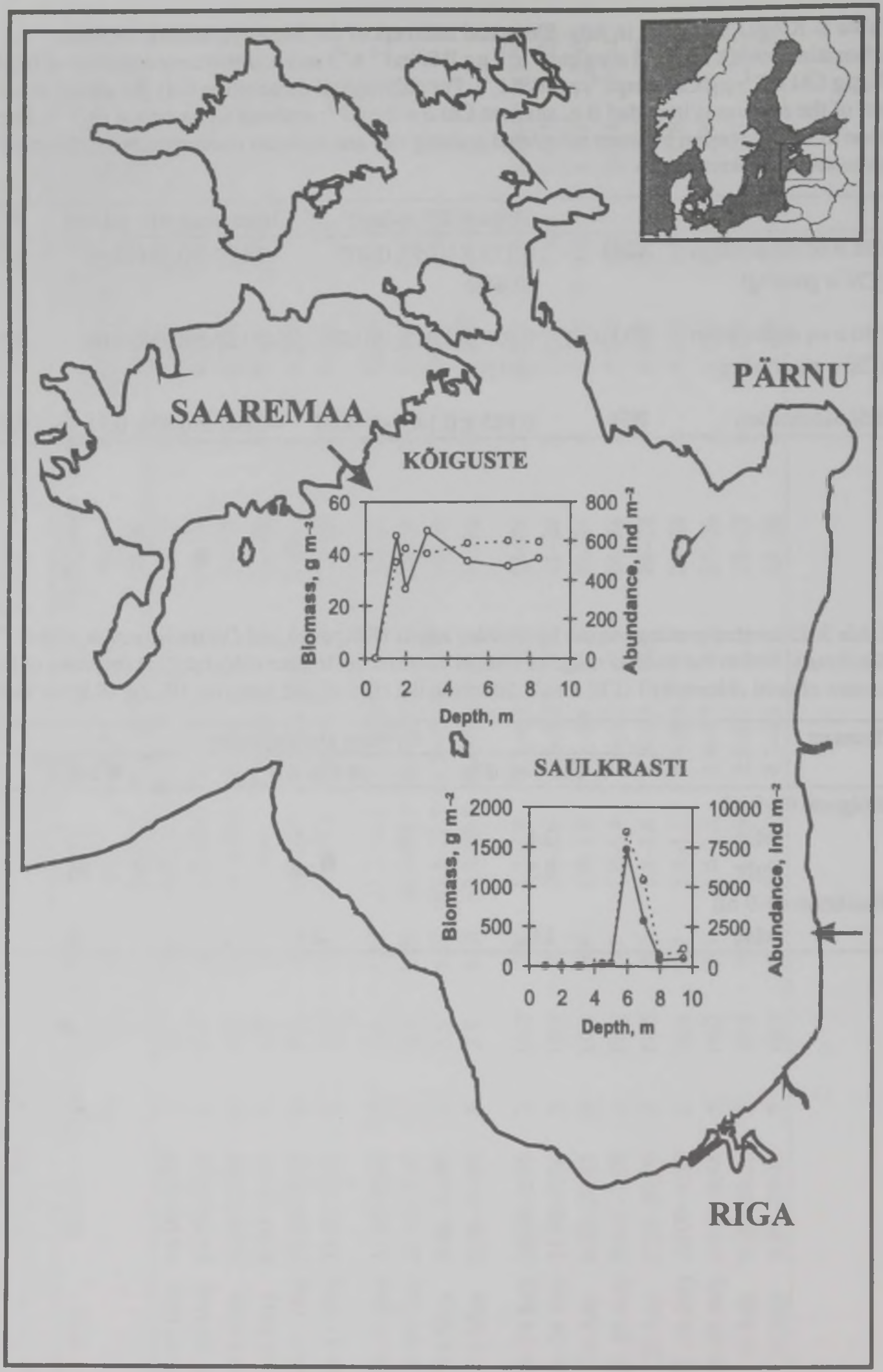

Figure 1. Study area. Arrows indicate the location of transects. Solid line in the graphs show biomass distribution (g dry weight m^{-2}) and dotted line abundance distribution (ind m^{-2}) of *M. edulis* (at Kõiguste) and *D. polymorpha* (at Saulkrasti) by depth.

Figure 2. Experimental cage used for the measurement of biodeposition rates of the mussels.

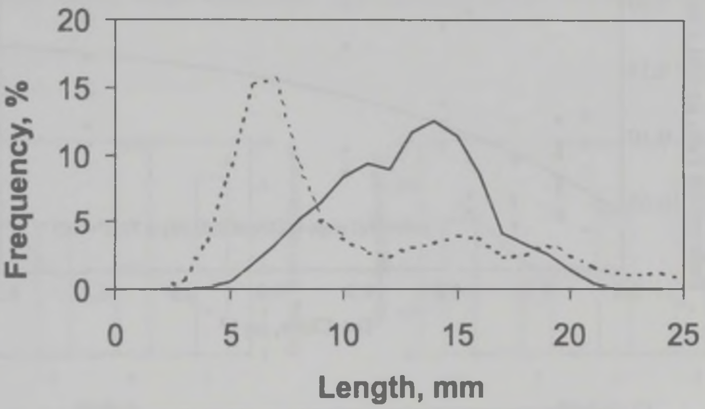

Figure 3. Population length-frequency distribution of *M. edulis* (broken line) and *D. polymorpha* (solid line) in the Gulf of Riga during 1996.

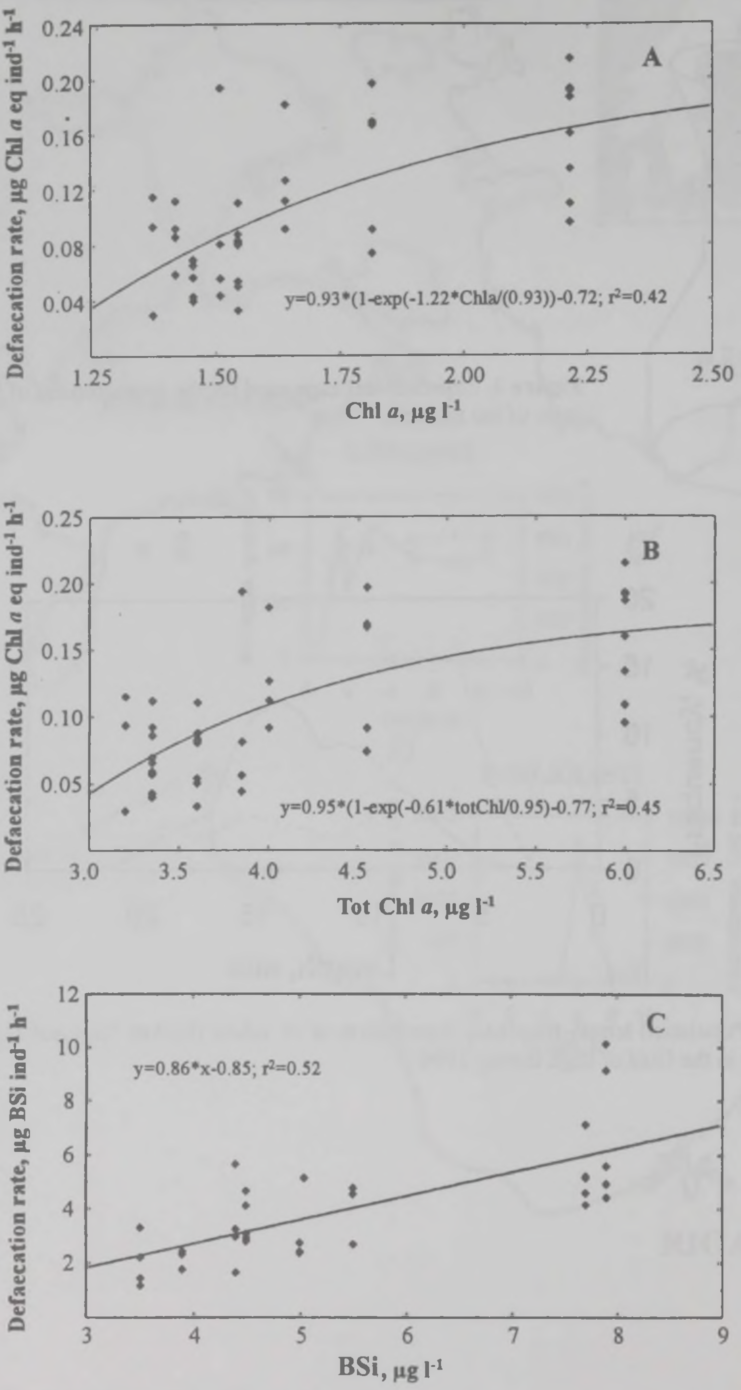

Figure 4. Defaecation rate in *Mytilus edulis* at Kõiguste in July as a function of ambient concentration of chlorophyll *a* (A), total chlorophyll *a* (B) and biogenic silicate (C). Each value represents the defaecation rate of 3 individuals. Equations of fitted functions are shown.

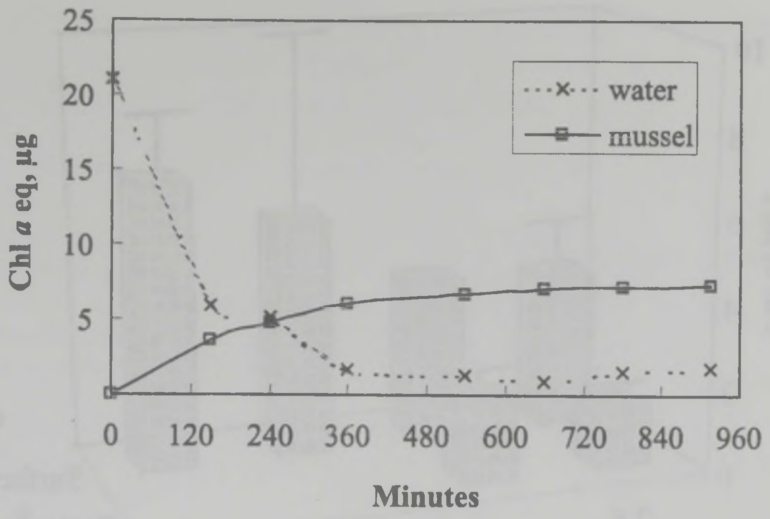

Figure 5. Temporal variation of total chlorophyll content in water and accumulated defaecation of total chlorophyll during budget experiment. The loss amounted to 61.4% after 9–15 hours of incubation.

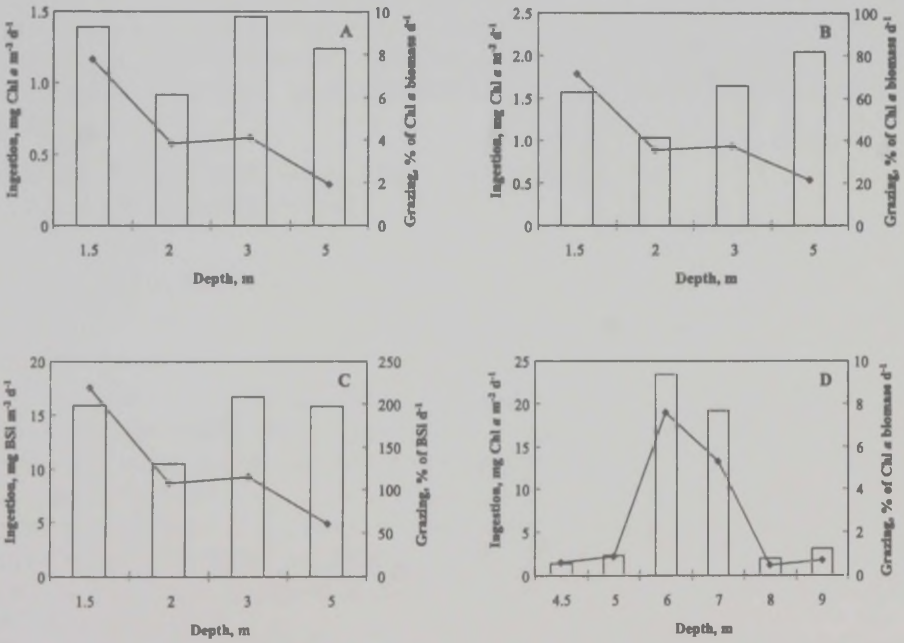

Figure 6. Population grazing rate (bars) and grazing impact (line) on the standing stock of chlorophyll *a* and biogenic silicate of the mussel population. A: Kõiguste May; B: Kõiguste July; C: Kõiguste July; D: Saulkrasti May. Standing stocks of chlorophyll were obtained from depth integrated samples taken daily at 2, 5 and 10 m stations (Møhlenberg unpubl.).

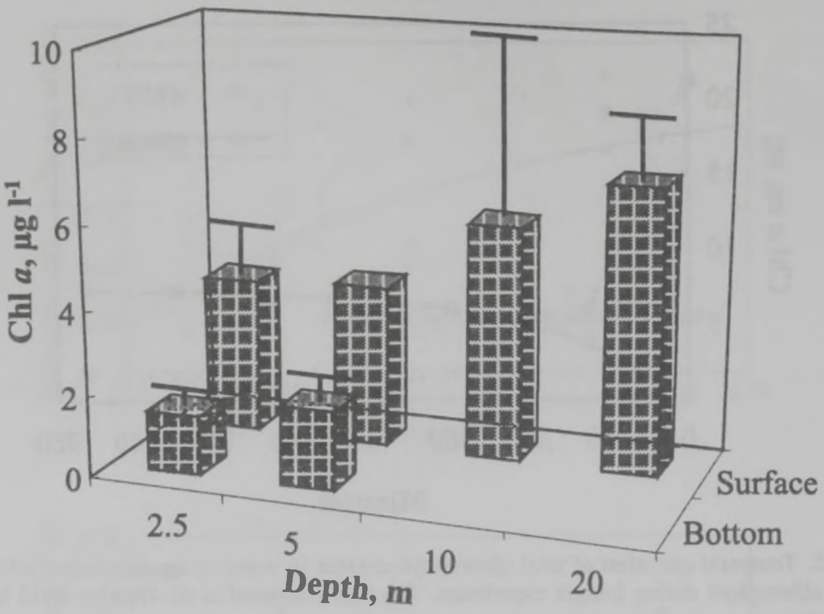

Figure 7. Spatial distribution of chlorophyll *a* in the littoral zone of Kõiguste in July. Bottom values from Table 1. Surface values were obtained from a synoptic study (Møhlenberg unpubl.). Average concentration and SD shown.

II

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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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*
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1. INTRODUCTION

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 (*e.g.* KANGAS *et al.*, 1982; RÖNNBERG *et al.*, 1985; SALEMAA, 1987; VOGT and SCHRAMM, 1991). This decline was attributed to the lower competitiveness of *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 *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 *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 Kõiguste 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. Kõiguste 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 Kõiguste 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 cm^2. 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 Kõiguste 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 Kõiguste 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 × 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 Kõiguste 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, m) and daily net increment (P, % of dw d^{-1}) of *Pilayella* in October is as follows:

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

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 $p_{\text{plant}} < 0.001$, $p_{\text{month}} < 0.001$, $p_{\text{plant×month}} < 0.001$, 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 $p_{\text{plant}} = 0.074$, $p_{\text{month}} < 0.001$, $p_{\text{plant×month}} < 0.001$, $n = 60$). *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 $p_{\text{species}} < 0.001$, $p_{\text{species×month}} < 0.001$, $p_{\text{species×month×light}} = 0.022$, 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

In the present study the data obtained from Phytobenthos Monitoring Programme financed by the Estonian Ministry of the Environment were used. The study was carried out within the framework of Estonian Governmental Programme no. 0200792s98 and NORFA project no. 96.30.002-M. We acknowledge L. Kautsky for her comments concerning the experimental procedures.

6. REFERENCES

Barnes, R. S. K. and R. N. Hughes, 1988: An introduction to marine ecology. — Blackwell Scientific Publications, Oxford, 305 pp.

Brawley, S. H. and W. H. Adey, 1981: Micrograzers may affect macroalgal density. — Nature **292**: 167–177.

Edgar, G. J., 1983: The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. — J. Exp. Mar. Biol. Ecol. **70**: 205–255.

Hacker, S. D. and L. P. Madin, 1991: Why habitat architecture and colour are important to shrimps living in pelagic Sargassum: Use of camouflage and plant-part mimicry. — Mar. Ecol. Prog. Ser. **70**: 143–155.

Hawkins, S. J. and R. G. Hartnoll, 1983: Grazing of intertidal algae by marine invertebrates. — Oceanogr. Mar. Biol. Annu. Rev. **21**: 195–282.

Hiscock, K. and R. Hoare, 1973: A portable suction sampler for rock epibiota. — Helgol. Meeresunters. **25**: 35–38.

Holmlund, M. B., C. H. Peterson and M. E. Hay, 1990: Does algal morphology affect amphipod susceptibility to fish predation? — J. Exp. Mar. Biol. Ecol. **139**: 65–83.

Jansson, A. M., 1974: Community structure, modelling and simulation of the *Cladophora* ecosystem in the Baltic Sea. — Contrib. Askö Lab. Univ. Stockholm **5**: 1–130.

Jansson, A. M., N. Kautsky, J. A. von Oertzen, W. Schramm, B. Sjöstedt, T. von Wachenfelddt and I. Wallentinus, 1982: Structural and functional relationships in a southern Baltic *Fucus* ecosystem — a joint study by the BMB Phytobenthos Group. — Contrib. Askö Lab. Univ. Stockholm **28**: 1–95.

Kangas, P., 1972: Quantitative sampling equipment for the littoral benthos. II. — IBP i Norden **10**: 9–16.

Kangas, P., H. Autio, G. Hällfors, H. Luther, Å. Niemi and H. Salemaa, 1982: A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–1981. — Acta Bot. Fenn. **118**: 1–27.

Kautsky, U. and H. Kautsky, 1995: Coastal productivity in the Baltic Sea. — *In*: Eleftheriou, A., A. D. Ansell and C. J. Smith (Eds.): Biology and ecology of shallow coastal waters, pp. 31–38. Olsen & Olsen, Fredensborg.

Lubchenco, J., 1978: Plant species diversity in a marine intertidal community: Importance of herbivore food preferences and algal competitive abilities. — Am. Nat. **112**: 23–39.

Lubchenco, J., 1982: Effects of grazers and algal competitors on fucoid colonization in tide pools. — J. Phycol. **18**: 544–550.

Lubchenco, J., 1983: *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. — Ecology **64**: 1116–1123.

Lubchenco, J. and B. A. Menge, 1978: Community development and persistence in a low rocky intertidal zone. — Ecol. Monogr. **59**: 67–94.

Malm, T., 1999: Distribution patterns and ecology of Fucus serratus L. and Fucus vesiculosus L. in the Baltic Sea. — Doctoral dissertation, University of Stockholm, Sweden, 130 pp.

Masterson, J. A. F., 1998: Investigations of the effects of macrophyte structure, food resources and health on habitat selection and refuge value in vegetated aquatic systems. — Doctoral dissertation, Florida Institute of Technology, USA, 145 pp.

Menge, B. A., 1976: Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. — Ecol. Monogr. **46**: 355–496.

Nicotri, M. E., 1980: Factors involved in herbivore food preference. — J. Exp. Mar. Biol. Ecol. **42**: 13–26.

Paalme, T., 1997: Primary production estimates with different macroalgal species in 1993–1994. — *In*: Ojaveer, E. (Ed.): Proceedings of the 14th Baltic Marine Biologists Symposium, pp. 184–194. Estonian Academy Publishers, Tallinn.

PAALME, T. and A. MÄKINEN, 1997: Variation in primary productivity of different Baltic macroalgal species in different seasons. — NorFa project report No. 9630.002–M, Nordisk Forskerutdanningsakademi, Oslo.

PAINE, R. T., 1974: Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. — Oecologia **15**: 93–120.

PEDERSEN, M. F. and J. BORUM, 1996: Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. — Mar. Ecol. Prog. Ser. **142**: 261–272.

RAVANKO, O., 1969: Benthic algae as a food for some invertebrates in the inner part of the Baltic. — Limnologica **7**: 203–205.

ROBERTSON, A. I. and K. H. MANN, 1980: The role of isopods and amphipods in the initial fragmentation of eelgrass detritus in Nova Scotia, Canada. — Mar. Biol. **59**: 63–69.

RÖNNBERG, O., J. LEHTO and I. HAAHTELA, 1985: Recent changes in the occurrence of *Fucus vesiculosus* in the Archipelago Sea, SW Finland. — Ann. Bot. Fenn. **22**: 231–244.

SALEMAA, H., 1979: Ecology of *Idotea* spp. (Isopoda) in the northern Baltic. — Ophelia **18**: 133–150.

SALEMAA, H., 1987: Herbivory and microhabitat preferences of *Idothea* spp. (Isopoda) in the northern Baltic Sea. — Ophelia **27**: 1–15.

SOKAL, R. R. and F. J. ROHLF, 1981: Biometry. The principles and practice of statistics in biological research. — W.H. Freeman, San Francisco, California, 859 pp.

STRICKLAND, J. D. H., 1960: Measuring the production of marine phytoplankton. — Bull. Fish. Res. Bd. Can., **122**: 1–172.

SUURSAAR, Ü., 1995: Nutrients in the Gulf of Riga. — *In*: OJAVEER, E. (Ed.): Ecosystem of the Gulf of Riga between 1920 and 1990. Academia **5**: 41–50.

VOGT, H. and W. SCHRAMM, 1991: Conspicuous decline of *Fucus* in Kiel Bay (western Baltic): What are the causes? — Mar. Ecol. Prog. Ser. **69**: 189–194.

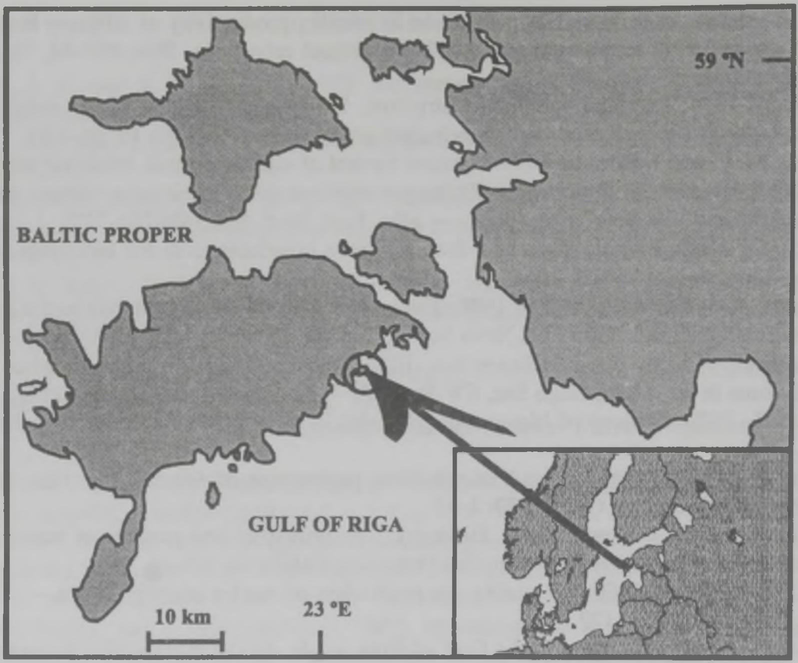


Figure 1. Study area. The circle shows the location of Kõiguste Bay.

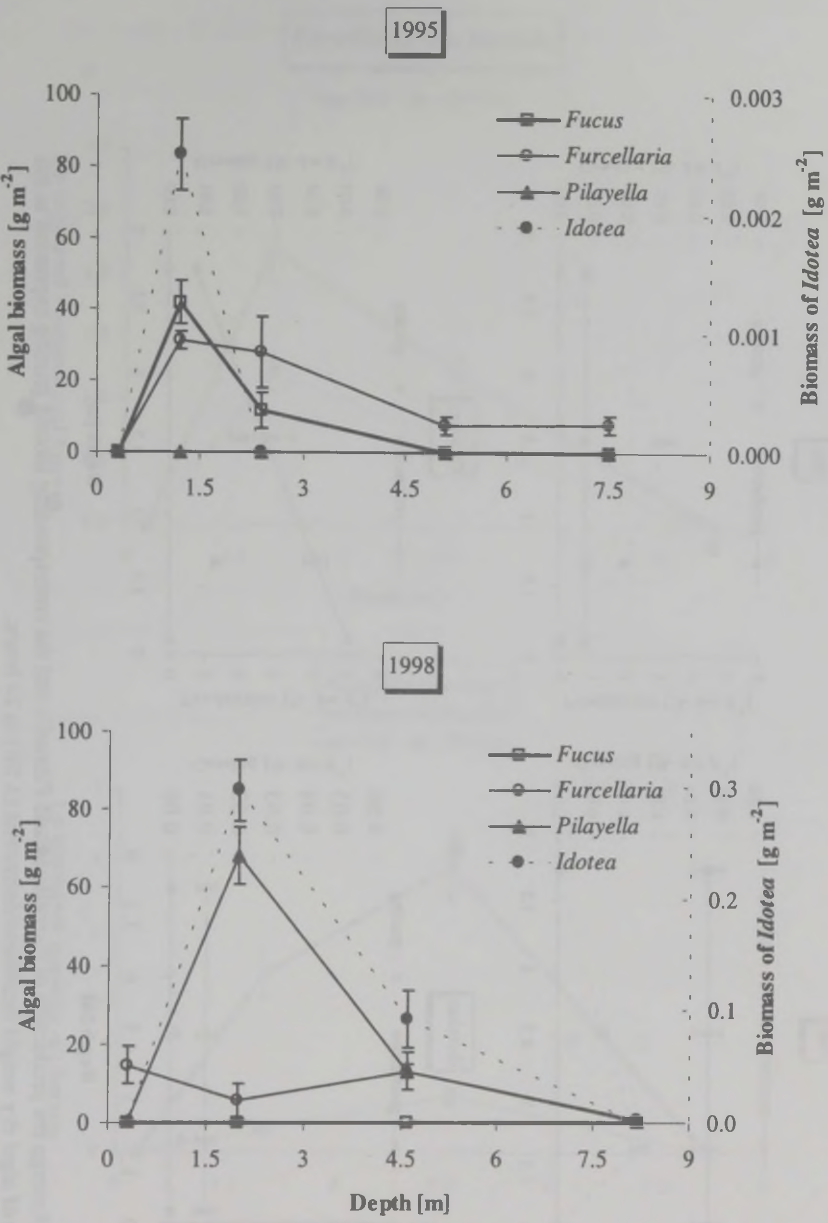


Figure 2. Average biomass distribution (g dw m^{-2} ± SE) of dominant macroalgal and herbivore species in Kõiguste Bay during 1995 and 1998.

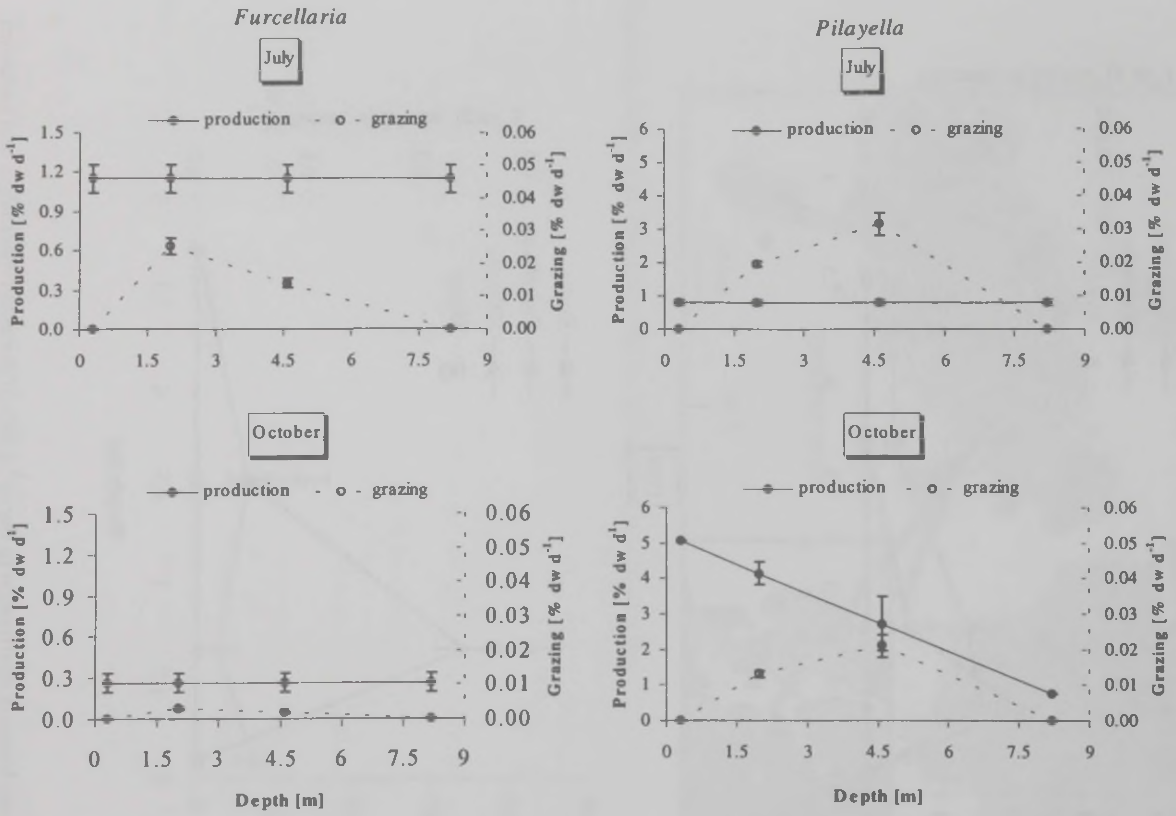


Figure 3. Average net production of *Furcellaria* and *Pilayella* and the corresponding idoteid grazing expressed as the percentage of algal dry weight increment/decrement (± SE) in 24 hours.

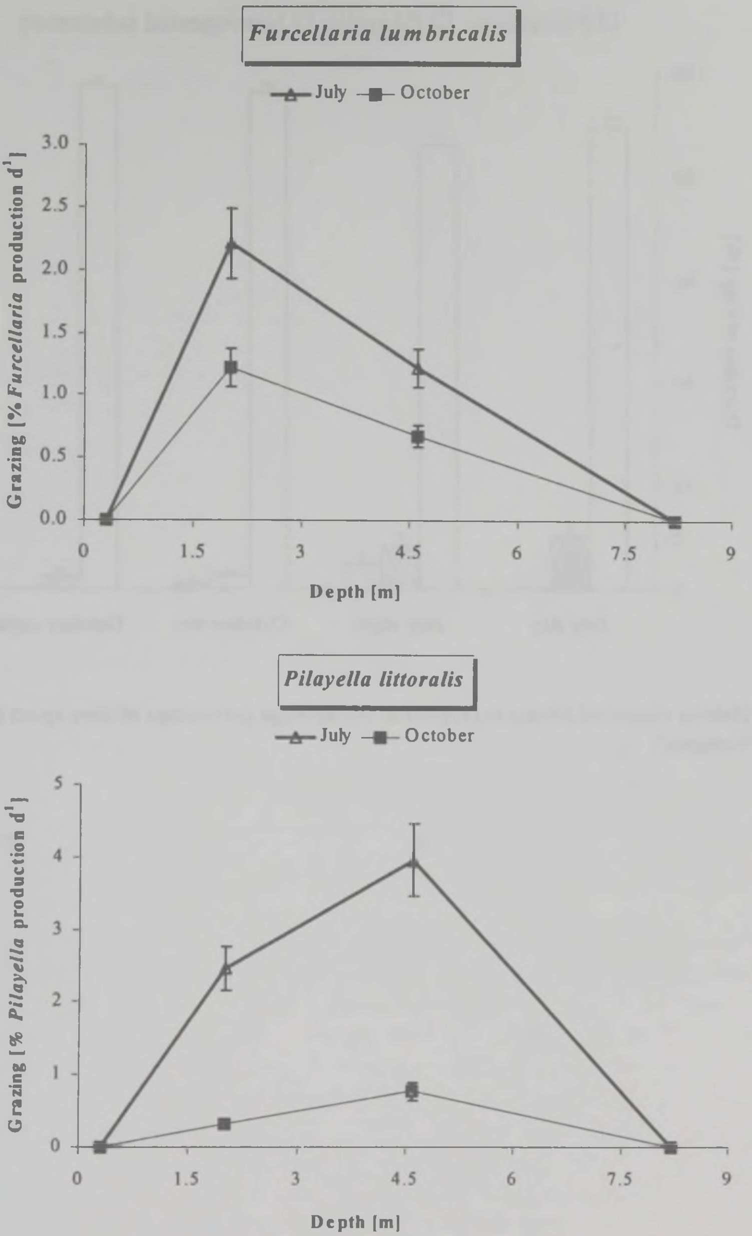


Figure 4. Average percentage of algal daily net production consumed by *Idotea* (± SE).

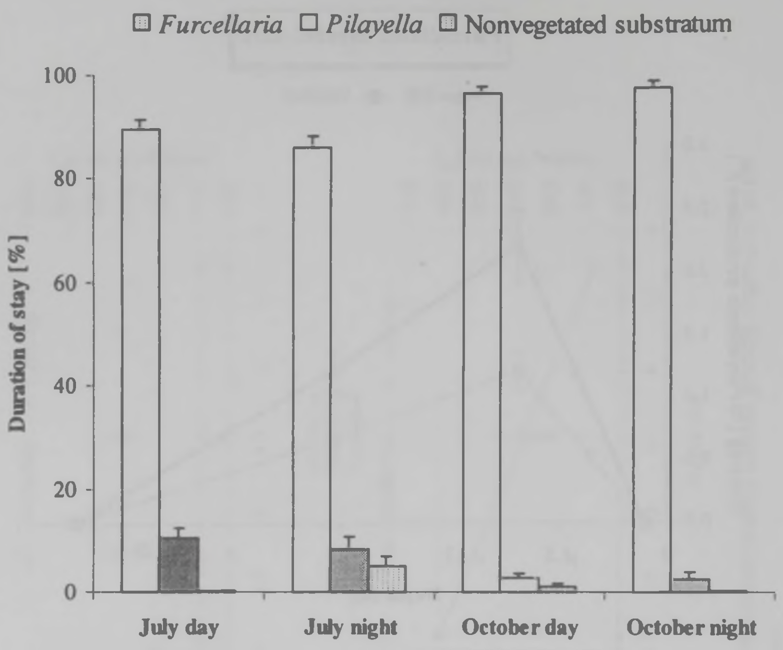


Figure 5. Habitat choice of *Idotea* expressed as the average percentage of time spent (± SE) in different "biotopes".

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).

COMPETITION FOR FOOD BETWEEN THE INTRODUCED POLYCHAETE *MARENZELLERIA VIRIDIS* AND THE RESIDENT AMPHIPOD *MONOPOREIA AFFINIS* IN THE BALTIC SEA

Jonne Kotta & Emil Ólafsson

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, Ólafsson & 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, Ólafsson & 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, Haahtela

1990, Leonardsson 1991, Hill & Elmgren 1992, Aarnio *et al.* 1998, Ejdung 1998). Consequently, high fluctuations in their density have drastic repercussions for the whole ecosystem.

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 cm^2), 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

M. viridis on the weight of juveniles was contradictory being either positive (no feeding) or negative (feeding).

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. *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 *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.

DISCUSSION

M. viridis had a clear negative effect on adult *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^{-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 *M. affinis* lose weight immediately after the spring bloom (Cederwall 1977). This may explain the poorer performance of weight over the length of *M. affinis* in discriminating inter- and intra-specific competition.

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 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 *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 *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 *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 *M. viridis* on the amphipod *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 (Haahtela 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.

REFERENCES

Aarnio K, Bonsdorff E, Norkko A (1998). Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. Mar Ecol Prog Ser 163:145–153.

Aarnio K, Bonsdorff E, Rosenback N (1996). Food and feeding habits of juvenile flounder *Platichtys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Åland Archipelago, northern Baltic Sea. J Sea Res 36:311–320.

Aarnio K, Sandberg E, Bonsdorff E (1991). Benthic predation on shallow-water macro- and meiofauna in the Baltic Sea: an experimental comparison between *Potamoschistus minutus* (Pisces) and *Saduria entomon* (Crustacea). Ann Zool Fenn 28:41–48.

Abrams PA, Hill C, Elmgren R (1990). The functional response of the predatory polychaete, *Harmothoe sarsi*, to the amphipod, *Pontoporeia affinis*. Oikos 59:261–269.

Aneer G (1975). Composition of food of the Baltic herring (*Clupea harengus v membras* L.), fourhorn sculpin (*Myoxocephalus quadricornis* L.) and eel-pout (*Zoarces viviparus* L.) from deep soft bottom trawling in the Askö–Landsort area during two consecutive years. Merentutkimuslait Julk 239:146–154.

Atkins SM, Jones AM, Garwood PR (1987). The ecology and reproductive cycle of a population of *Marenzelleria viridis* (Annelida: Polychaeta: Spionidae) in the Tay Estuary. Proc R Soc Edinburgh 92B:311–322.

Barnes RSK & Hughes RN (1988). An Introduction to Marine Ecology. Second edition. Blackwell Scientific publications, Oxford.

Begon M, Harper JL, Townsend CR (1996). Ecology. Individuals, Populations and Communities. Blackwell Science, Oxford.

Blomqvist S & Lundgren L (1996). A benthic sled for sampling soft bottoms. Helgol Meeresunters 50:453–456.

Cederwall H (1977). Annual macrofauna production of a soft bottom in the northern Baltic Proper. In Keegan BF, Ceidigh PO, Boaden PJS (eds) Biology of Benthic Organisms. Proc 11th Europ Mar Biol Symp. Pergamon Press, Oxford, 155–164.

Ejdung G (1998). Behavioural responses to chemical cues of predation risk in a three-link Baltic Sea food chain. Mar Ecol Prog Ser 165:137–144.

Ejdung G & Elmgren R (1998). Predation on newly settled bivalves by deposit-feeding amphipods: a Baltic Sea case study. Mar Ecol Prog Ser 168:87–94.

Elmgren R (1978). Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna. Kieler Meeresforsch 4:1–22.

Elmgren R, Ankar S, Marteleur B, Ejdung G (1986). Adult interference with post-larvae in soft sediments: the *Pontoporeia-Macoma* example. Ecology 67:827–836.

Essink K & Kleef HL (1993). Distribution and life cycle of the north American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. Netherlands J Aq Ecol 27:237–246.

Guillard RL (1975). Culture of phytoplankton for feeding marine invertebrates. In Smith WL, Chanley MH (eds) Culture of Marine Invertebrate Animals. Plenum Press, New York, 29–60.

Haahtela I (1990). What do Baltic studies tell us about the isopod *Saduria entomon* (L.)? Ann Zool Fenn 27:269–278.

Hill C (1992). Interactions between year classes in the benthic amphipod *Monoporeia affinis*: effects on juvenile survival and growth. Oecologia 91:157–162.

Hill C & Elmgren R (1987). Vertical distribution in the sediment in the co-occurring benthic amphipods *Pontoporeia affinis* and *P. femorata*. Oikos 49:221–229.

Hill C & Elmgren R (1992). Predation by the isopod *Saduria entomon* on the amphipods *Monoporeia affinis* and *Pontoporeia femorata*: experiments on prey vulnerability. Oecologia 91:153–156.

Hill C, Elmgren R, Abrams P (1990). Predation by the polychaete *Harmothoe sarsi* on different size classes of the amphipod *Pontoporeia affinis*. In Barnes M, Gibson RN (eds) Trophic Relationships in the Marine Environment. Proc. 24th Europ. Mar. Biol. Symp. Aberdeen University Press, 468–477.

Järvekülg A (1973). Distribution and ecology of local populations of benthic glacial relicts. Oikos Suppl 15:91–97.

Järvekülg A (1979). Bottom Fauna of the Eastern Baltic Sea. Valgus, Tallinn (in Russian). [Yarvekyulg, A. Donnaya fauna vostochnoj chasti Baltijskogo morya]

Kester DR, Duedall IW, Connors DN, Pykovocz RM (1967). Preparation of artificial seawater. Limnol Oceanogr 12:176–179.

Kotta J & Kotta I (1998). Distribution and invasion ecology of *Marenzelleria viridis* in the Estonian coastal waters. Proc Estonian Acad Sci Biol Ecol 47:212–220.

Kube J, Gosselck F, Powilleit M (1997). Long-term changes in the benthic communities in the Pomeranian Bay (southern Baltic Sea). Helgol Meeresunters 51:399–416.

Lehtonen K, Andersin A-B (1998). Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. Mar Ecol Prog Ser 168:71–85.

Leonardsson K (1991). Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Isopoda). Ecology 72:1273–1285.

Leonardsson K (1994). Multiple density dependence in two sub-populations of the amphipod Monoporeia affinis: A potential for alternative prey. Oecologia 97:26–34.

Levinton JS (1972). Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am Nat 106:472–486.

Levinton JS (1979). Deposit feeders, their resources, and the study of resource limitation. In Livingston RJ (ed) Ecological Processes in Coastal and Marine Systems. Plenum Press, New York, 117–141.

Ólafsson E & Elmgren R (1991). Effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: a laboratory approach. Mar Ecol Prog Ser 74:99–107.

Ólafsson E & Elmgren R (1997). Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. Estuar Coast Shelf Sci 45:149–164.

Ólafsson E & Moore CG (1990). Control of meiobenthic abundance by macroepifauna in a subtidal muddy habitat. Mar Ecol Prog Ser 65:241–249.

Ólafsson EB & Persson L-E (1986). The interaction between *Nereis diversicolor* O.F. Müller and *Corophium volutator* Pallas as a structuring force in a shallow brackish sediment. J Exp Mar Biol Ecol 103:103–117.

Ólafsson EB, Peterson CH, Ambrose WG Jr (1994). Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. Oceanogr Mar Biol Annu Rev 32:65–109.

Sarvala J (1986). Interannual variation of growth and recruitment in Pontoporeia affinis (Lindström) (Crustacea: Amphipoda) in relation to abundance fluctuations. J Exp Mar Biol Ecol 101:41–59.

Sarvala J & Uitto A (1991). Production of benthic amphipods *Pontoporeia affinis* and *P. femorata* in a Baltic archipelago. Ophelia 34:71–90.

Segerstråle S (1937). Studien über die Bodentierwelt in südfinnländischen Küstengewässern, V: Das reife *Pontoporeia affinis*-Männchen ("P. weltneri") als Saisonnahrung für der Stint (*Osmerus eperlanus* L.). Commentat Biol Soc Sci Fennica 7:1–17.

Segerstråle S (1957). Baltic Sea. Mem Geol Soc Am 67:757–800.

Sokal RR & Rohlf FJ (1981). Biometry. W.H. Freeman & Company, San Francisco.

Uitto A & Sarvala J (1990). Perspectives on the ecological factors regulating *Pontoporeia* populations in the northern Baltic Sea. Ann Zool Fenn 27:297–301.

Uitto A & Sarvala J (1991). Seasonal growth of the benthic amphipods *Pontoporeia affinis* and *Pontoporeia femorata* in a Baltic archipelago in relation to environmental factors. Mar Biol 111:237–246.

Zettler ML (1996). Successful establishment of the spionid polychaete, *Marenzelleria viridis* (Verrill, 1873), in the Darss-Zingst estuary (southern Baltic) and its influence on the indigeneous macrozoobenthos. Arch Fish Mar Res 43:273–284.

Zettler ML (1997). Bibliography on the genus *Marenzelleria* and its geographical distribution, principal topics and nomenclature. Aq Ecol 31:233–258.

Zettler ML, Bick A, Bochert R (1995). Distribution and population dynamics of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water of southern Baltic. Arch Fish Mar Res 42:209–224.

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

Treatment	*M. affinis*		*M. viridis*	Feeding
	Density	Age	Density	
1	20	ad	2	+
2	20	ad	2	–
3	20	juv	2	+
4	20	juv	2	–
5	40	ad	2	+
6	40	ad	2	–
7	40	juv	2	+
8	40	juv	2	–
9	80	ad	2	+
10	80	ad	2	–
11	80	juv	2	+
12	80	juv	2	–
13	20	ad	0	+
14	20	ad	0	–
15	20	juv	0	+
16	20	juv	0	–
17	40	ad	0	+
18	40	ad	0	–
19	40	juv	0	+
20	40	juv	0	–
21	80	ad	0	+
22	80	ad	0	–
23	80	juv	0	+
24	80	juv	0	–

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).

Source of variation	df	F	P
***Monoporeia* juveniles**			
SURVIVAL			
A: *Marenzelleria*	1	0.02	ns
B: Denstity	2	0.09	ns
C: Food	1	1.41	ns
WEIGHT			
A: *Marenzelleria*	1	0.38	ns
B: Denstity	2	3.31	0.046
C: Food	1	72.77	<0.001
LENGTH			
A: *Marenzelleria*	1	2.78	ns
B: Denstity	2	3.05	0.048
C: Food	1	109.61	<0.001
***Monoporeia* adults**			
SURVIVAL			
A: *Marenzelleria*	1	0.37	ns
B: Denstity	2	1.58	ns
C: Food	1	1.41	ns
WEIGHT			
A: *Marenzelleria*	1	1.03	ns
B: Denstity	2	3.43	0.040
C: Food	1	27.34	<0.001
LENGTH			
A: *Marenzelleria*	1	3.41	0.049
B: Denstity	2	1.89	ns
C: Food	1	6.95	0.011
Marenzelleria			
SURVIVAL	2	0.12	ns
A: Density	1	0.43	ns
B: Age	1	0.43	ns
C: Food			

ns is equivalent to p>0.05

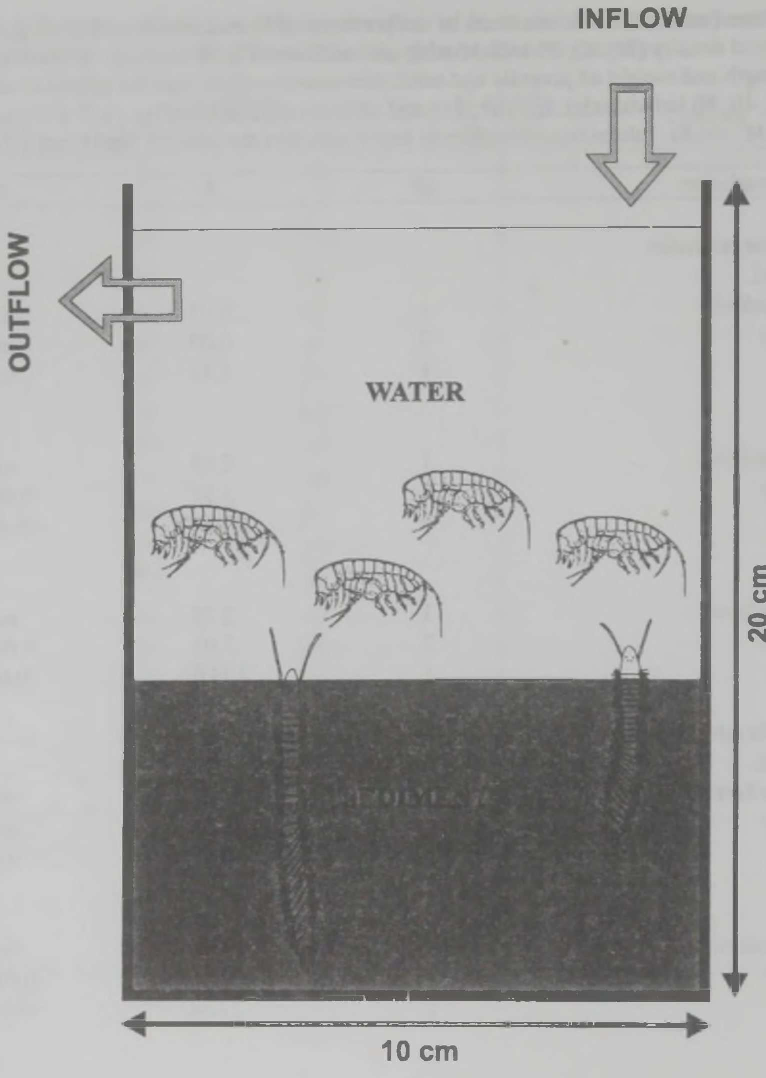


Figure 1. Experimental setup.

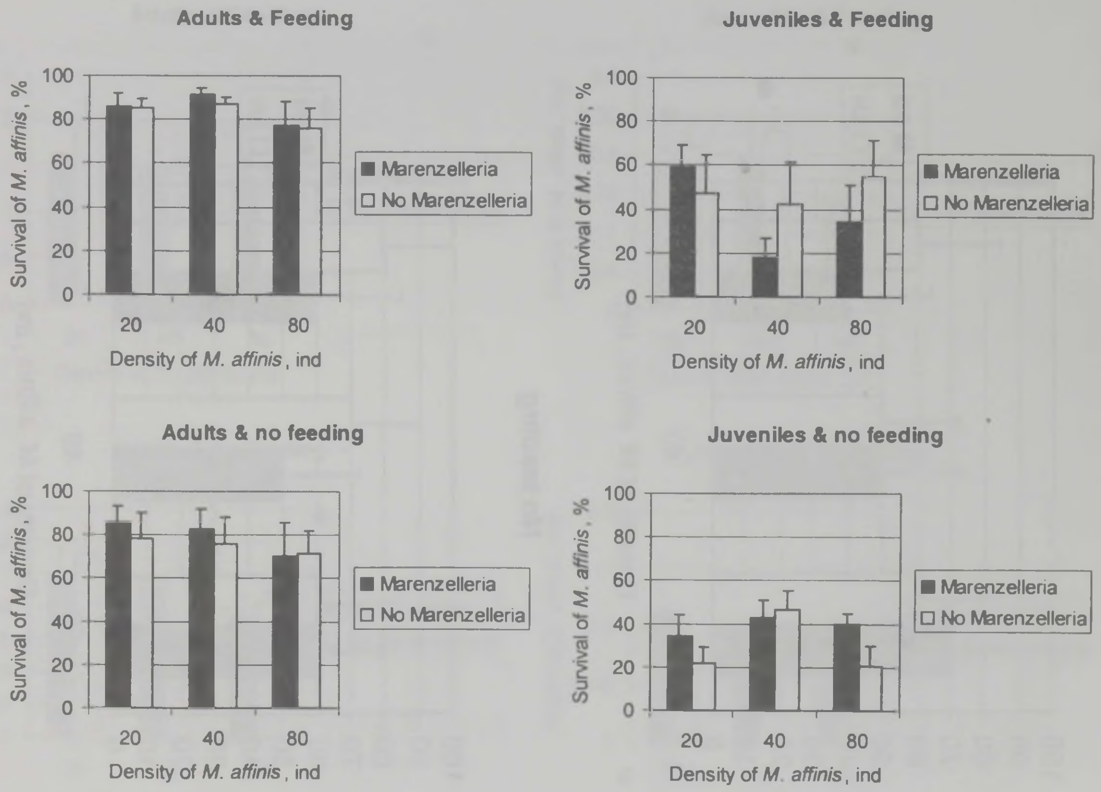


Figure 2. Survival of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*.

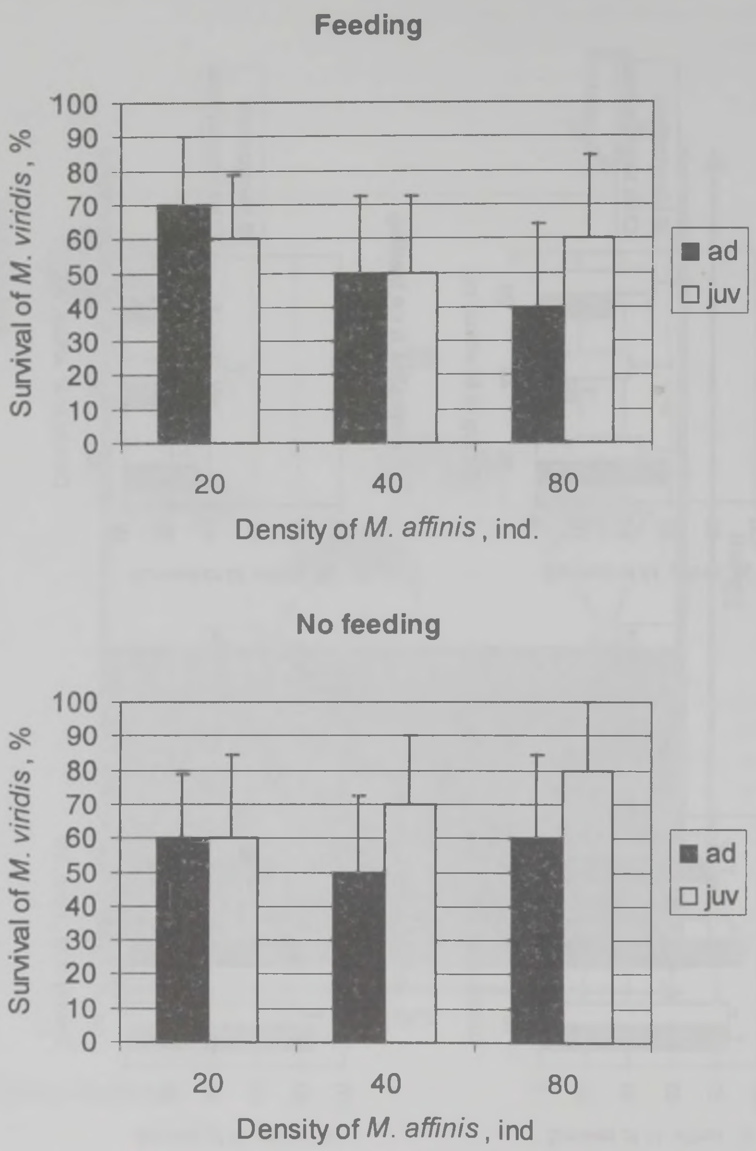


Figure 3. Survival of *M. viridis* in relation to feeding, amphipod age (juv – juveniles, ad – adults) and density.

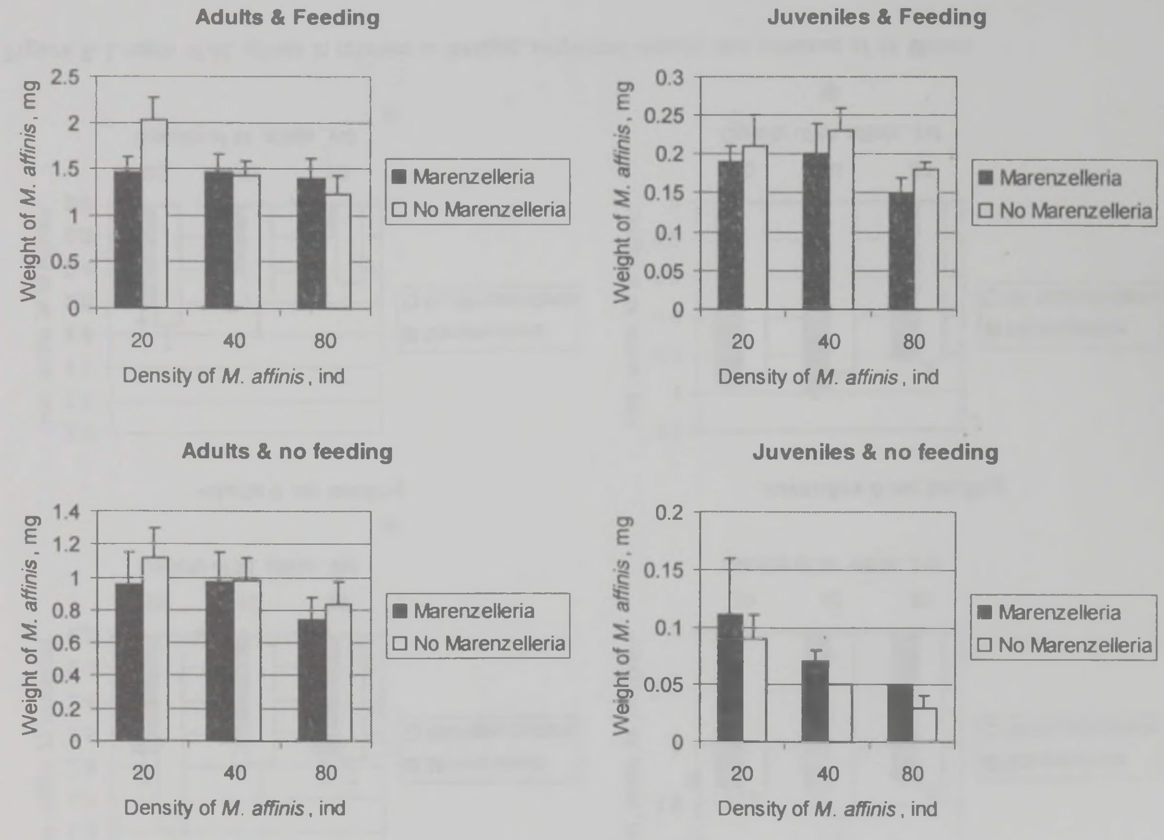
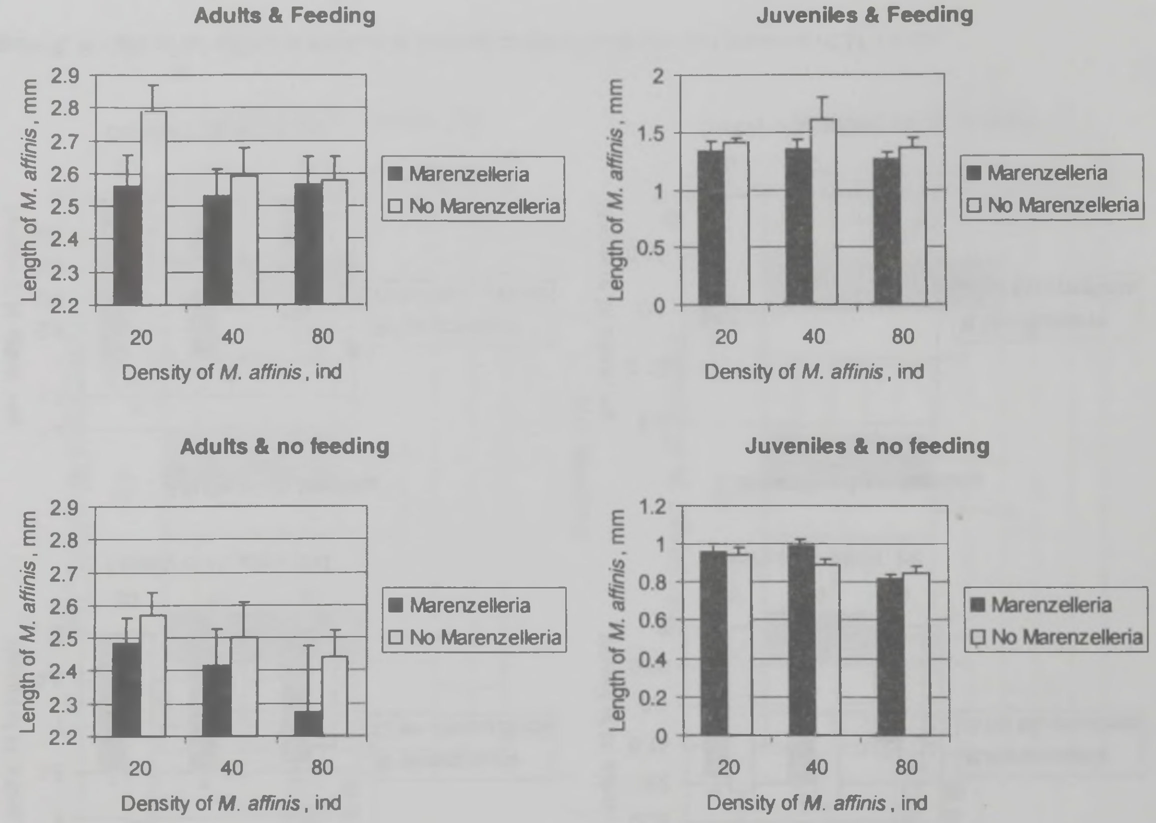


Figure 4. Weight of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*.


Adults & Feeding

Juveniles & Feeding

Adults & no feeding

Juveniles & no feeding

Figure 5. Length of *M. affinis* in relation to feeding, amphipod density and presence of *M. viridis*.

IV

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Effect of diffuse and point source nutrient supply
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EFFECT OF DIFFUSE AND POINT SOURCE NUTRIENT SUPPLY ON THE LOW DIVERSE MACROZOOBENTHIC COMMUNITIES OF THE NORTHERN BALTIC SEA

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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 waterbodies. 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 dissapearance 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 Òlafsson 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 km^2) 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 km^2) 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 m^2) in the coastal sea of Saaremaa in 1993 and in Seurasaari in 1995. An Ekman-Lenz bottom sampler (0.04 m^2) 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 fuviatilis* 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, Cructacea, 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. Macrozoobenthic 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.

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REFERENCES

Andersin A.-B. 1986. The question of eutrophication in the Baltic Sea — results from a long-term study of the macrozoobenthos in the Gulf of Bothnia. *Vesientutkimuslait. Julk., Helsinki/Publ. Water Res. Inst., Helsinki* 68: 102–106.

Andersin A.-B. & Sandler H. 1991. Macrobenthic fauna and oxygen deficiency in the Gulf of Finland. *Memoranda Soc. Fauna Flora Fennica* 67: 3–10.

Barnes R.S.K. & Hughes R.N. 1988. *An introduction to marine ecology*. Second edition. Blackwell Scientific publications, Oxford, 305 pp.

Bonsdorff E., Aarnio K. & Sandberg E. 1991. Temporal and spatial variability of zoobenthic communities in the archipelago waters of the northern Baltic Sea — consequences of eutrohication? *Int. Revue ges. Hydrobiol.* 76: 433–449.

Bonsdorff E., Blomqvist E.M., Mattila J. & Norkko A. 1997. Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuarine, Coastal and Shelf Sci.* 44 (Supplement A): 63–72.

Bray J.B. & Curtis J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27: 325–349.

Brey T. 1986. Increase in macrozoobenthos above the halocline in Kiel Bay comparing the 1960s with the 1980s. *Mar. Ecol. Prog. Ser.* 28: 299–302.

Cederwall H. & Elmgren R. 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea. *Ophelia (Suppl. 1)*: 31–48.

Clarke K.R. & Warwick R.M. 1994. *Changes in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory, Plymouth.

Elmgren R. 1989. Mans impact on the ecosystem of the Baltic Sea. Energy flows today and at the turn of the century. *Ambio* 18: 326–332.

Järvekülg A. 1979. *Benthic fauna in the eastern part of the Baltic Sea*. Valgus, Tallinn, 382 pp. (In Russian.)

Josefson A.B. & Widbom B. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Mar. Biol.* 100: 31–40.

Kautsky H., Kautski L., Kautski N., Kautski U. & Lindblad C. 1992. Studies on the *Fucus vesiculosus* community in the Baltic Sea. *Acta Phytogeogr. Suec.* 78: 33–48.

Kautsky H., Martin G., Mäkinen A., Borgiel M., Vahteri P. & Rissanen J. 1999. Structure of phytobenthic and associated animal communities in the Gulf of Riga. *Hydrobiologia* 393: 191–200.

Kautsky N., Kautski H., Kautski U. & Waern M. 1986. Decreased depth penetration of *Fucus vesiculosus* L. since the 1940's indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28: 1–8.

Kotta I. & Kotta J. 1997. 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. In: Ojaveer E. (ed.), *Proceedings of the 14th Baltic Marine Biologists Symposium*, Estonian Academy Publishers, Tallinn, pp. 70–79.

Laine A.O., Sandler H., Andersin A.-B. & Stigzelius, J. 1997. Long-term changes of macrozoobenthos in the Eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. *J. Sea Res.* 38: 135–159.

Larsson U., Elmgren R. & Wulff F. 1985. Eutrophication and the Baltic Sea: Causes and consequences. *Ambio* 14: 9–14.

Launiainen J., Pokki J., Vainio J., Niemimaa I. & Voipio A. 1989. Long-term changes in the Secchi depth in the northern Baltic Sea (In Finnish with English abstract). *XIV Geofüsikan päivät Helsinki*, pp. 117–121.

Leppäkoski E. 1975. Assessment of the degree of pollution on the basis of macrozoobenthos in marine and brackish-water environments. *Acta Academiae Aboensis, Ser B, Matematic, naturvetenskaper, teknik* 35: 1–90.

Mägi L. & Lips U. 1998. Budget components of water, salt, and nutrients in the Gulf of Riga in 1993–95. *Proc. Estonian Acad. Sci. Biol. Ecol.* 47: 14.31.

Modig H. & Òlafsson E. 1998. Responses of Baltic benthic invertebrates to hypoxic events. *J. Exp. Mar. Biol. Ecol.* 229: 133–148.

Nixon S.W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199–219.

Pearson T.H. & Rosenberg R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology. An Annual Review* 16: 229–311.

Pesonen L., Norha T., Rinne I., Viljamaa H. 1994. Helsingin ja Espoon merialueiden velvoitetarkkailu vuonna 1993. *Helsingin Kaupungin Ympäristökeskuksen Julkaisuja* 6: 1–115.

Ratas U. & Nilson E. 1997. *Small islands of Estonia*. Institute of Ecology, Tallinn, 232 pp.

Rosenberg R. & Loo L.-O. 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia* 29: 213–225.

Sokal R.R. & Rohlf F.J. 1981. Biometry. *The principles and practice of statistics in biological research*. Second edition. W.H. Freeman, San Francisco, 859 pp.

Warwick R.M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Mar. Biol.* 92: 557–562.

Warwick R.M. & Clarke K.R. 1991. A comparison of some methods for analysing changes in benthic community structure. *J. mar. biol. Ass. U.K.* 71: 225–244.

Warwick R.M., Pearson T.H. & Ruswahyuni 1987. Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. *Mar. Biol.* 95: 193–200.

Welsh B.L. 1980. Comparative nutrient dynamics of a marsh-mudflat ecosystem. *Estuarine Coastal Mar. Sci.* 10: 143–164.

Wilson K.A., Able K.W. & Heck J.K.L. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Mar. Ecol. Prog. Ser.* 58: 243–251.

Yurkovskis A., Wulff F., Rahm L., Andrushaitis, A. & Rodrigues-Medina M. 1993. A nutrient budget of the Gulf of Riga, Baltic Sea. *Estuarine, Coastal and Shelf Sci.* 37: 113–127.

Zmudzinski L. & Osowiecki A. 1991. Long-term changes in macrozoobenthos of the Gdansk Deep. *Int. Revue ges. Hydrobiol.* 76: 465–471.

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.

Region	No	Depth (m)	Sediment		
			Clay	Silt	Mixed
Saaremaa isolated	12	1.53 (0.5–2.5)	58.3	16.7	25.0
Seurasaari isolated	13	3.96 (1.5–10)	30.8	23.1	46.1
Saaremaa open	8	2.63 (0.5–6)	37.5	12.5	50.0
Vuosaari open	10	5.30 (3–10)	40.0	10.0	50.0

Table 2. Probability intervals of two-way analysis of variance ($\alpha = 0.05$) for the abundances and biomasses of macrozoobenthos against isolation rank (open, isolated) and region (Saaremaa, Helsinki).

	Model	Isolation	Region	Interaction
Biomass	total	0.476	**0.035**	0.102
	Vermes	0.522	0.205	0.641
	Crustacea	0.288	0.286	0.288
	Insecta	0.484	0.106	0.700
	Mollusca	0.458	**0.041**	0.104
Abundance	total	**0.024**	**0.013**	**0.041**
	Vermes	**0.031**	**0.004**	**0.017**
	Crustacea	0.632	0.095	0.632
	Insecta	0.054	0.981	0.782
	Mollusca	0.709	**0.000**	0.279

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.

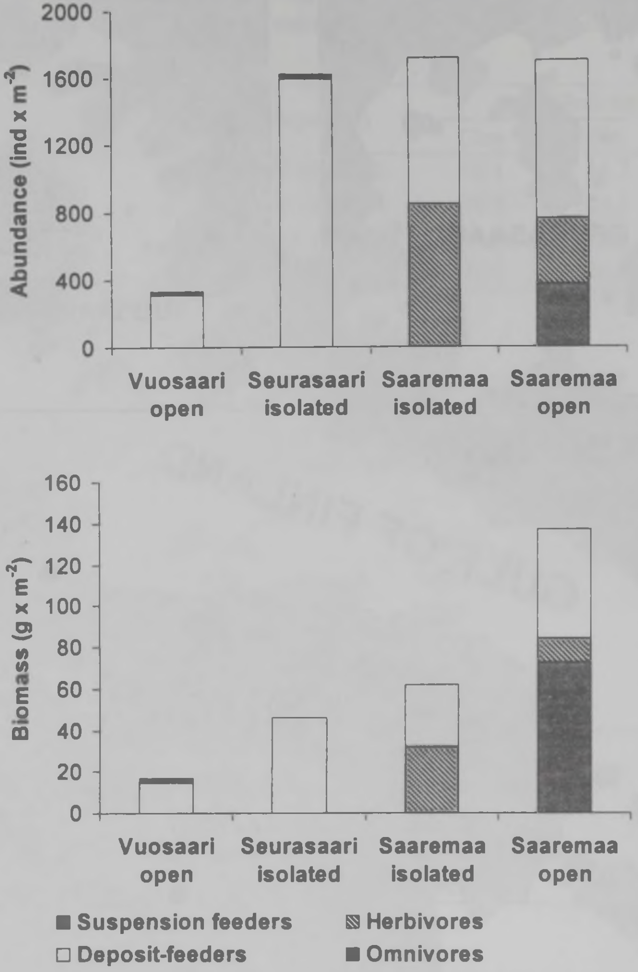

Figure 2. Share of different trophic groups within zoobenthic communities in the coastal sea of Helsinki and Saaremaa.

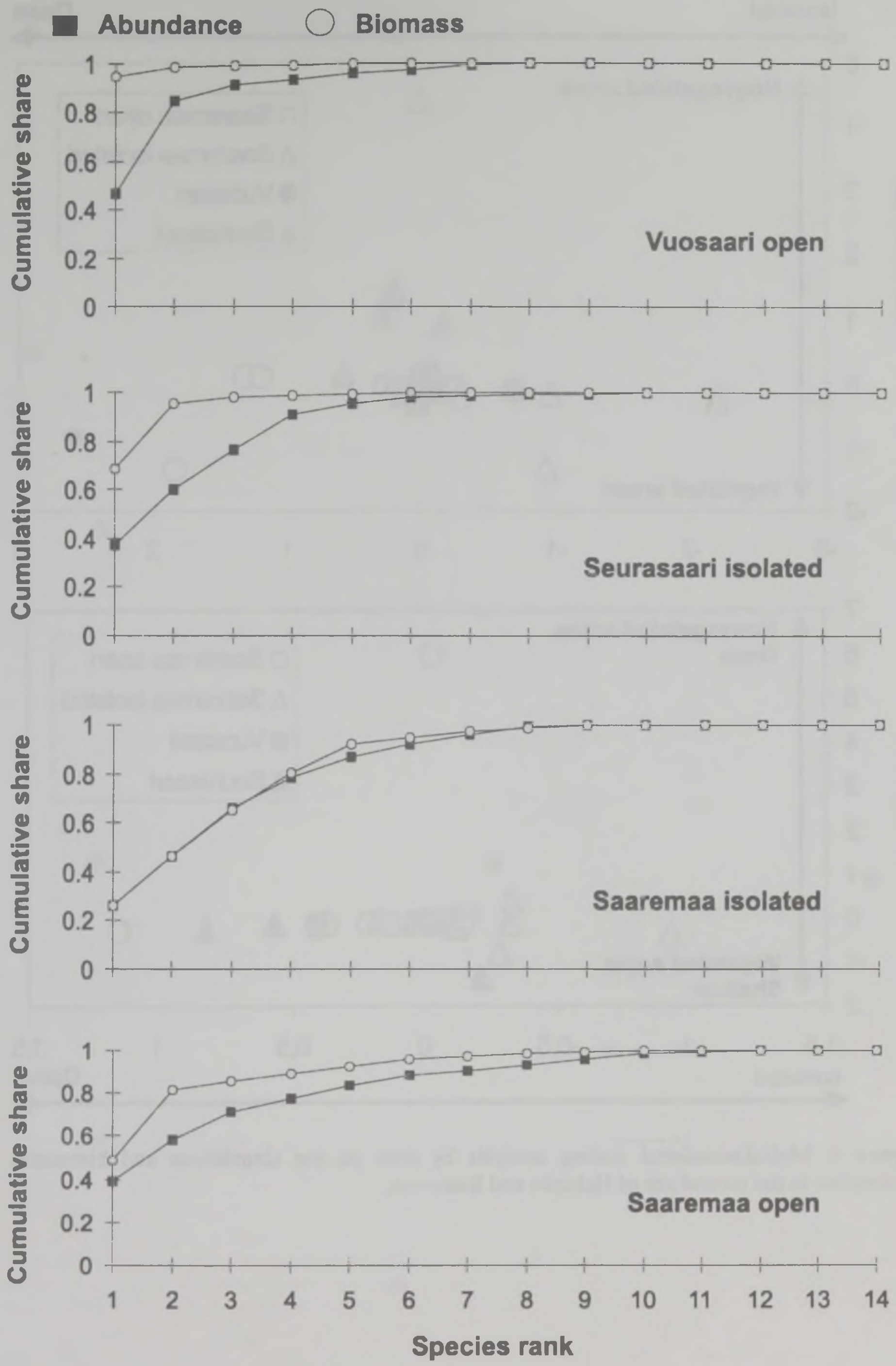

Figure 3. K-dominance curves of biomass and abundance of zoobenthic communites in the study area.

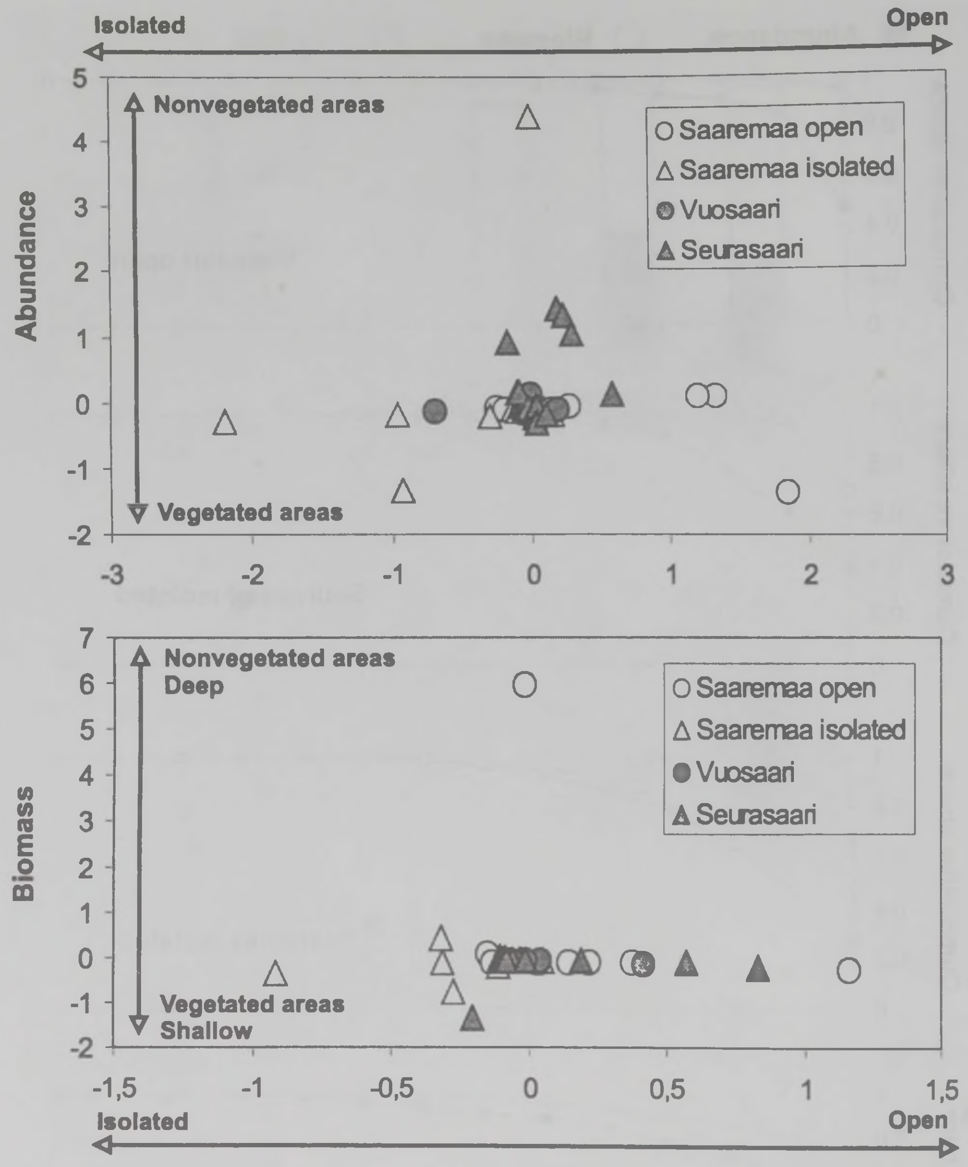

Figure 4. Multidimensional scaling analysis by sites on the abundances and biomasses of zoobenthos in the coastal sea of Helsinki and Saaremaa.

V

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I. & Lumberg, A. 1999.
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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.

Key words: abiotic and biotic components, alien species, Gulf of Riga ecosystem, long-term changes.

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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).

We provide new data from the extensive studies of the ecosystem of the Gulf of Riga since the 1970s. Some of these data represent a continuation of long-term studies of the abundance and population structure of specific fish species and the abundance of mysids. In addition, new integrated investigations were started of food resources and the feeding activity of pelagic fish species.

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

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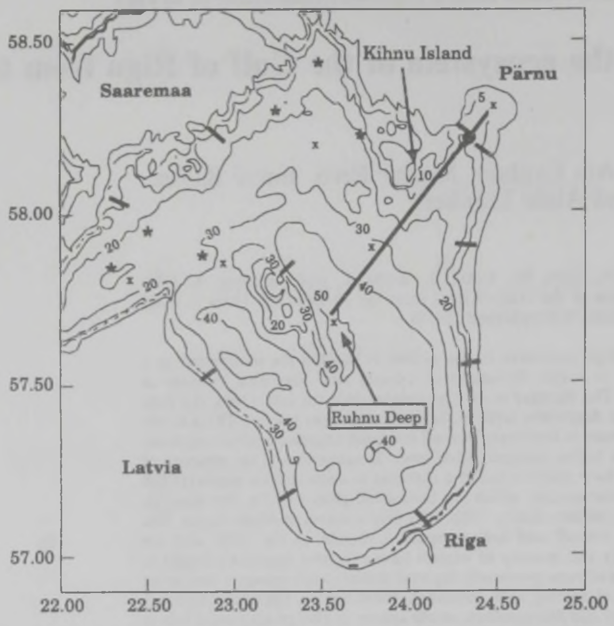

Figure 1. Location of sampling stations in the Gulf of Riga along the transect fished during experimental bottom-trawl surveys from Pärnu Bay to Ruhnu Deep. Crosses denote single sites and short solid lines indicate transects for zoobenthos sampling. Filled circle shows sampling location of *Neomysis integer*. Additional sampling locations for *Cercopagis pengoi* are given by asterisks.

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 m^2 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:

$$\log(\text{mean catch} + 1) = \text{year} + \text{month} + \varepsilon, \qquad (1)$$

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 ε 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 relicts (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 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 m^3) 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 m^2), whereas a van Veen bottom grab (0.10 m^2) 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.

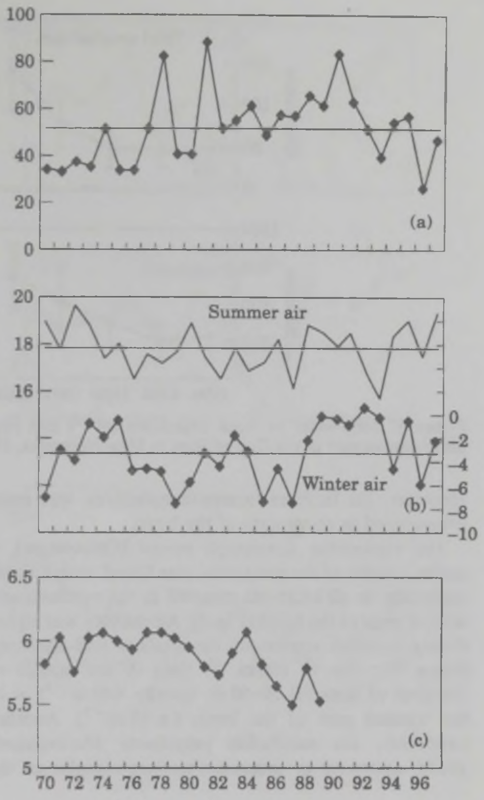

Figure 2. Time series of abiotic parameters, 1970–1998 (data from Estonian Hydrometeorological Institute): (a) freshwater inflows (m^3/s) *via* Pärnu River; (b) mean air temperature, December–March, and summer water temperature (°C), June–August, in Pärnu Bay; and (c) mean salinity in the north-eastern part of the Gulf of Riga, June–December.

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.

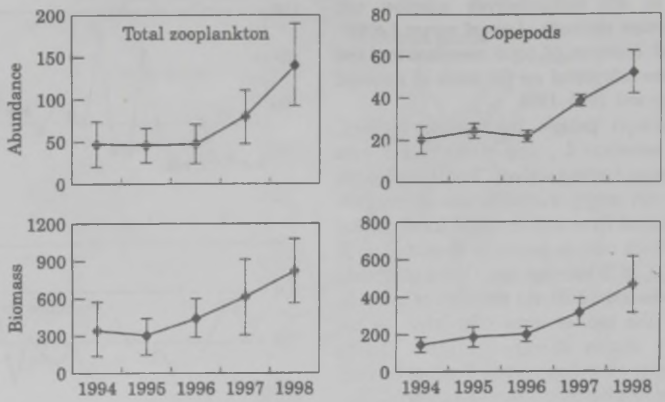

Figure 3. Time series of mean abundance (m^{-3}) and biomass (mg m^{-3}) of the total zooplankton and copepods in the north-eastern part of the Gulf of Riga in May–November, 1994–1998 (bars denote standard errors).

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 ($\pm 10\ m^{-3}$). 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).

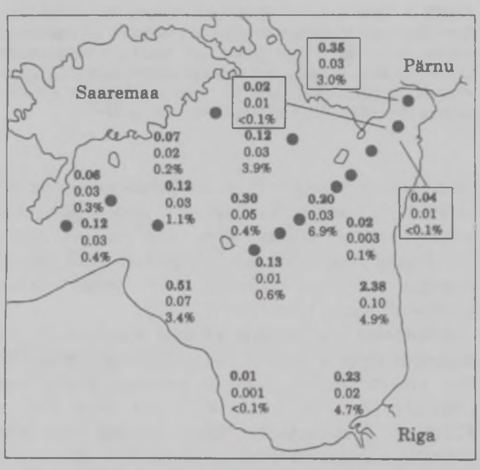

Figure 4. Catch locations of *Cercopagis pengoi* (filled circles) in 1994–1997. Biomass of *Marenzelleria viridis* (in bold; g dry weight m^{-3}), standard errors and the percentage contribution to the total biomass of macrozoobenthos (%) in the Gulf of Riga, 1994–1995.

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

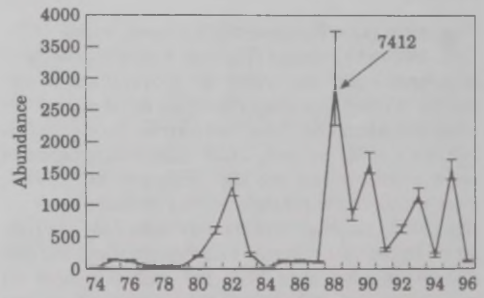

Figure 5. Time series of abundance (m^{-3}, ± s.e.) of *Neomysis integer* in the north-eastern part of the Gulf of Riga during autumn, 1974–1996.

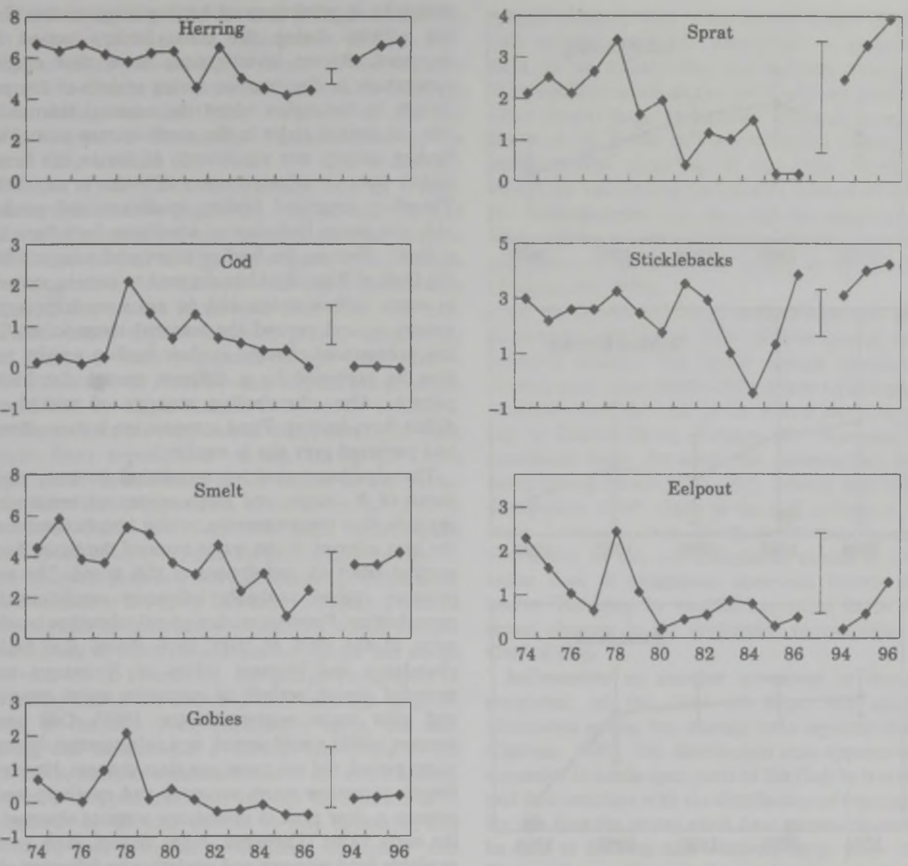

Figure 6. Dynamics of the abundance-based year effect for selected fish in the Gulf of Riga over the years 1974–1986 and 1994–1996. Bars indicate the least significant difference for each entire time series (2•s.e.).

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

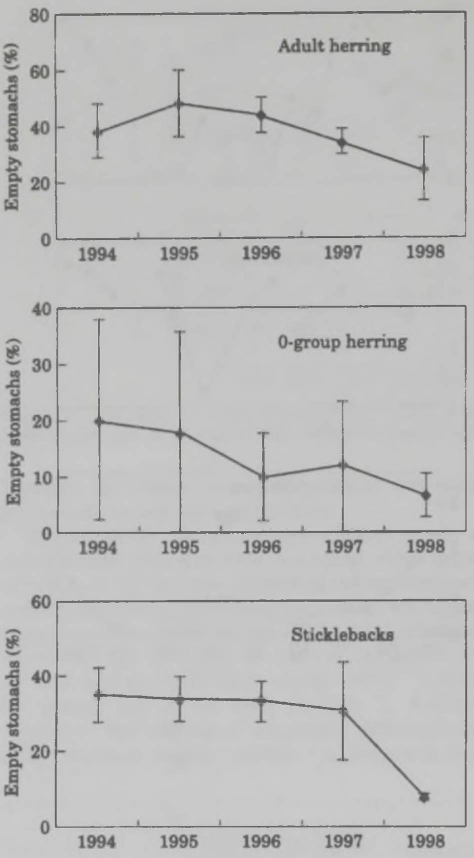

Figure 7. Percentage of empty stomachs (± s.e.) of adult and juvenile herring and three-spined stickleback in the Gulf of Riga during their main feeding period, 1994–1998.

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 *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 *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 *N. integer*. This might partly explain the higher abundance values generally recorded since the late 1980s compared to the 1970s. *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, *Osmerus eperlanus* 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 *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, sculpins, 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, lumpsucker, 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, 1995) 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.

Acknowledgements

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References

Andrushaitis, A., Seisuma, Z., Legzdina, M., and Lenshs, E. 1995. River load of eutrophying substances and heavy metals into the Gulf of Riga. *In* Ecosystem of the Gulf of Riga between 1920 and 1990, 2: Hydrochemistry, pp. 32–40. Ed. by E. Ojaveer. Estonian Academy Publishers, Tallinn. 277 pp.

Bagge, O. 1981. The yearly consumption of cod in the Baltic and Kattegat as estimated from stomach content. ICES CM 1981/J:27.

Carlton, J. 1996. Marine bioinvasions: the alteration of marine ecosystems by non-indigenous species. Oceanography, 9.

Erm, V. A. 1967. On the dynamics of pikeperch catches in Pärnu Bay and biologically justified regulation of its fishery. Rybokhozjaistvennye Issledovanie v Basseine Baltijskogo Morja, 3: 109–118 (in Russian).

Gaumiga, R., Berzinsh, V., and Urtans, E. 1997. Impact of environmental factors on the fish community of the Gulf of Riga. *In* Proceedings of the 13th Baltic Marine Biologists Symposium. Jurmala, Latvia, August 31–Sept. 4, 1993, pp. 205–210. Ed. by A. Andrushaitis. Institute of Aquatic Ecology, University of Latvia. 262 pp.

George, J. D. 1966. Reproduction and early development of the spionid polychaete, *Scolecolepides viridis* (Verrill). Biological Bulletin, 130: 76–93.

HELCOM 1996. Third Periodic Assessment of the State of the Marine Environment in the Baltic Sea, 1989–1993. Background document Baltic Sea Environment Proceedings No. 64 B. 252 pp.

Jermakovs, V. 1998. *Marenzellaria viridis* (Verrill, 1873) – new and important component of the Gulf of Riga benthos communities, p. 73. Book of abstracts. The Gulf of Riga Projekt 1993–1998. Symposium in Jurmala, Latvia, May 10–14, 1998. 122 pp.

Kornilovs, G. 1993. The modern state of Baltic herring spawning grounds in the Gulf of Riga. ICES CM 1993/J:26.

Kotta, I. 1995. Nektobenthos (Mysidacea). *In* Ecosystem of the Gulf of Riga between 1920 and 1990, pp. 187–195. Ed. by E. Ojaveer. Estonian Academy Publishers, Tallinn.277 pp.

Lehtonen, K., Cederwall, H., and Jermakovs, V. 1998. Seasonal fluctuations of growth, metabolism and chemical composition of some important macrozoobenthos species in the Gulf of Riga, p. 34. Book of abstracts. The Gulf of Riga Projekt 1993–1998. Symposium in Jurmala, Latvia, May 10–14, 1998. 122 pp.

Matthäus, W. 1993. Major inflows of highly saline water into the Baltic Sea – a review. ICES CM 1993/C:52.

Ojaveer, H. 1997. Composition and dynamics of fish stocks in the Gulf of Riga ecosystem. Dissertationes Biologicae Universitatis Tartuensis No. 31. Tartu University Press, Tartu. 138 pp.

Ojaveer, H., Lankov, A., Lumberg, A., and Turovski, A. 1997. Forage fishes in the brackish Gulf of Riga ecosystem (Baltic Sea). *In* Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, pp. 293–309 Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks. 816 pp.

Rannak, L. A. 1970. Herring *Clupea harengus membras* L. Doctoral thesis. Tartu. 77 pp.

Sidrevics, L., Line, R., Berzinsh, V., and Kornilovs, G. 1993. Long-term changes of zooplankton abundance in the Gulf of Riga. ICES CM 1993/L:15, 14 pp.

Simm, M. 1982. Zooplankton dynamics in Pärnu Bay suffering anthropogenic eutrophication. *In* Problemy sovremennoj ekologii, p. 10. Tartu (in Russian).

Suursaar, Ü. 1995. Nutrients in the Gulf of Riga. *In* Ecosystem of the Gulf of Riga between 1920 and 1990, 2: Hydrochemistry, pp. 41–50. Ed. by E. Ojaveer. Estonian Academy Publishers, Tallinn. 277 pp.

Suursaar, Ü., and Tenson, J. 1998. Hydrochemical regime and productivity of the Pärnu Bay in 1968–1996. *In* More Studies on the Water Exchange and the Nutrients of the Gulf of Riga, pp. 91–117. Ed. by Ü Suursaar and V. Astok. EMI Report Series, No. 9. Tallinn. 119 pp.

Uzars, D. 1975. Peculiarities of feeding and quantitative food consumption of eastern Baltic cod. ICES CM 1975/P:3

Uzars, D. 1985. Food composition in the Eastern Baltic cod for the 1963–1984 period. ICES CM 1985/J:3.

Uzars, D. 1994. Feeding of cod (*Gadus morhua callarias* L.) in the Central Baltic in relation to environmental changes. ICES Marine Science Symposia, 198: 612–623.

Zmudzinski, L. 1996. The effect of the introduction of the American species *Marenzelleria viridis* (*Polychaeta*: Spionidae) on the benthic ecosystem of Vistula Lagoon. Marine Ecology, 17: 221–226.

VI

Kotta, J. & Orav, H.
Factors affecting the distribution, abundance and
biomass of invertebrate fauna in the Väinameri (north-eastern Baltic Sea)
(submitted to *Ann. Zool. Fenn.*).

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 cm^2, Kangas 1972) on silty, sand or gravel bottoms and with a suction sampler (catching surface 315 cm^2, 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*.

ACKNOWLEDGEMENTS

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REFERENCES

Bick, A. & Burckhardt, R. 1989: Erstnahweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum. — *Mitt. Zool. Mus. Berl.* 65: 237–247.

Carlton, J. T. 1996: Pattern, process and prediction in marine invasion ecology. — *Biol. Conserv.* 78: 97–106.

Clarke, K. R. 1993: Non-parametric multivariate analyses of changes in community structure. — *Aust. J. Ecol.* 18: 117–143.

Clarke, K. R. & Green, R. H. 1988: Statistical design and analysis for a 'biological effects' study. — *Mar. Ecol. Prog. Ser.* 46: 213–226.

Clarke, K. R. & Warwick, R. M. 1994: *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation.* — Plymouth Marine Laboratory, UK. 144 pp.

Connel, J. H. 1978: Diversity in tropical rain forests and coral reefs. — *Science* 199: 1302–1310.

Essink, K. & Kleef, H. L. 1993: Distribution and life cycle of the North American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. — *Neth. J. Aq. Ecol.* 27: 237–246.

Gollasch, S. & Leppäkoski, E. 1999: *Initial Risk Assessment of Alien Species in Nordic Coastal Waters.* — Nordic Council of Ministers, Copenhagen. 244 pp.

Gray, J. S. 1997: Marine biodiversity: patterns, threats and conservation needs. — *Biodivers. Conserv.* 6: 153–175.

Hiscock, K. & Hoare, R. 1973: A portable suction sampler for rock epibiota. — *Helgol. Meeresunters.* 25: 35–38.

Jansson, K. 1994: *Alien Species in the Marine Environment. Introductions to the Baltic Sea and the Swedish west coast.* — Report 4357. Swed. Environ. Prot. Agency, Solna. 68 pp.

Järvekülg, A. 1970: Väinamere põhjaloomastik. — In: Kumari, E. (ed.), *Lääne-Eesti rannikualade loodus*: 42–60. Valgus, Tallinn.

Kangas, P. 1972: Quantitative sampling equipment for the littoral benthos. II. — *IBP i Norden* 10: 9–16.

Kautsky, N. & Evans, S. 1987: Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. — *Mar. Ecol. Prog. Ser.* 38: 201–212.

Kotta, J. & Kotta, I. 1998: Distribution and invasion ecology of *Marenzelleria viridis* in the Estonian coastal waters. — *Proc. Est. Acad. Sci. Biol. Ecol.* 47: 212–220.

Kotta, J., Orav, H. & Kotta, I. 1998: Distribution and filtration activity of the zebra mussel, *Dreissena polymorpha*, in the Gulf of Riga and the Gulf of Finland. — *Proc. Est. Acad. Sci. Biol. Ecol.* 47: 32–41.

Leppäkoski, E. 1991: Introduced species — resource or threat in brackish water seas? Examples from the Baltic and the Black Sea. — *Mar. Pollut. Bull.* 23: 219–223.

Levinton, J. S. 1972: Stability and trophic structure in deposit-feeding and suspension-feeding communities. — *Am. Nat.* 106: 472–486.

Mardiste, H. 1970: Väinameri. — In: Kumari, E. (ed.), *Lääne-Eesti rannikualade loodus*: 7–16. Valgus, Tallinn.

Mills, E. L., Leach, J. H., Carlton, J. T. & Secor, C. L. 1993: Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. — *J. Great Lakes Res.* 19: 1–54.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M. 1994: Declining biodiversity can alter the performance of ecosystems. — *Nature* 368: 734–737.

Norkko, A. & Bonsdorff, E. 1996a: Population responses of coastal zoobenthos to stress induced by drifting algal mats. — *Mar. Ecol. Prog. Ser.* 140: 141–151.

Norkko, A. & Bonsdorff, E. 1996b: Rapid zoobenthic community responses to accumulations of drifting algae. — *Mar. Ecol. Prog. Ser.* 131: 143–157.

Reusch, T. B. H. & Chapman, A. R. O. 1995: Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) beds. — *J. Exp. Mar. Biol. Ecol.* 192: 257–271.

Segerstråle, S. G. 1957: Baltic Sea. — *Mem. Geol. Soc. Am.* 67: 751–800.

Suursaar, Ü., Astok, V. & Otsmann, M. 1998: The front of Väinameri. — *Est. Mar. Inst. Rep. Ser.* 9: 23–33.

Trei, T. 1970: Väinamere põhjataimestik. — In: Kumari, E. (ed.), *Lääne-Eesti rannikualade loodus*: 27–41. Valgus, Tallinn.

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

Environmental variable	Abundance	Biomass
Latitude (Pos N)	–0.016	–0.061
Longitude (Pos E)	0.054	–0.002
Sediment	0.105	0.084
Depth	0.118	0.112
N tot in water	0.051	–0.013
P tot in water	0.050	–0.012
Water transparency	0.051	–0.013
Dominant macroalgae in the sample	0.195	0.195
Dominant macroalgae at the site	0.131	0.111
Coverage of macroalgae at the site	0.085	0.004

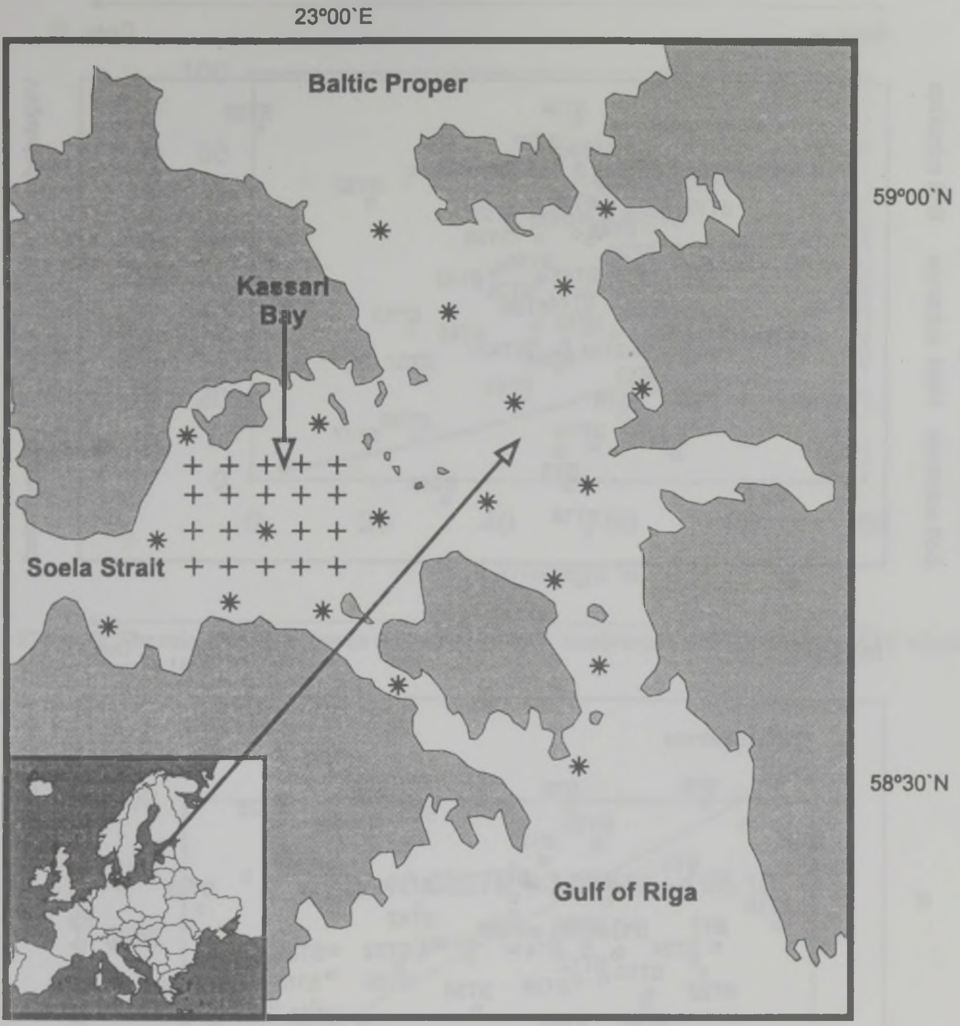

Figure 1. Study area. The stars represent the grid of sampling stations in the whole Väinameri area and the crosses that of Kassari Bay, respectively.

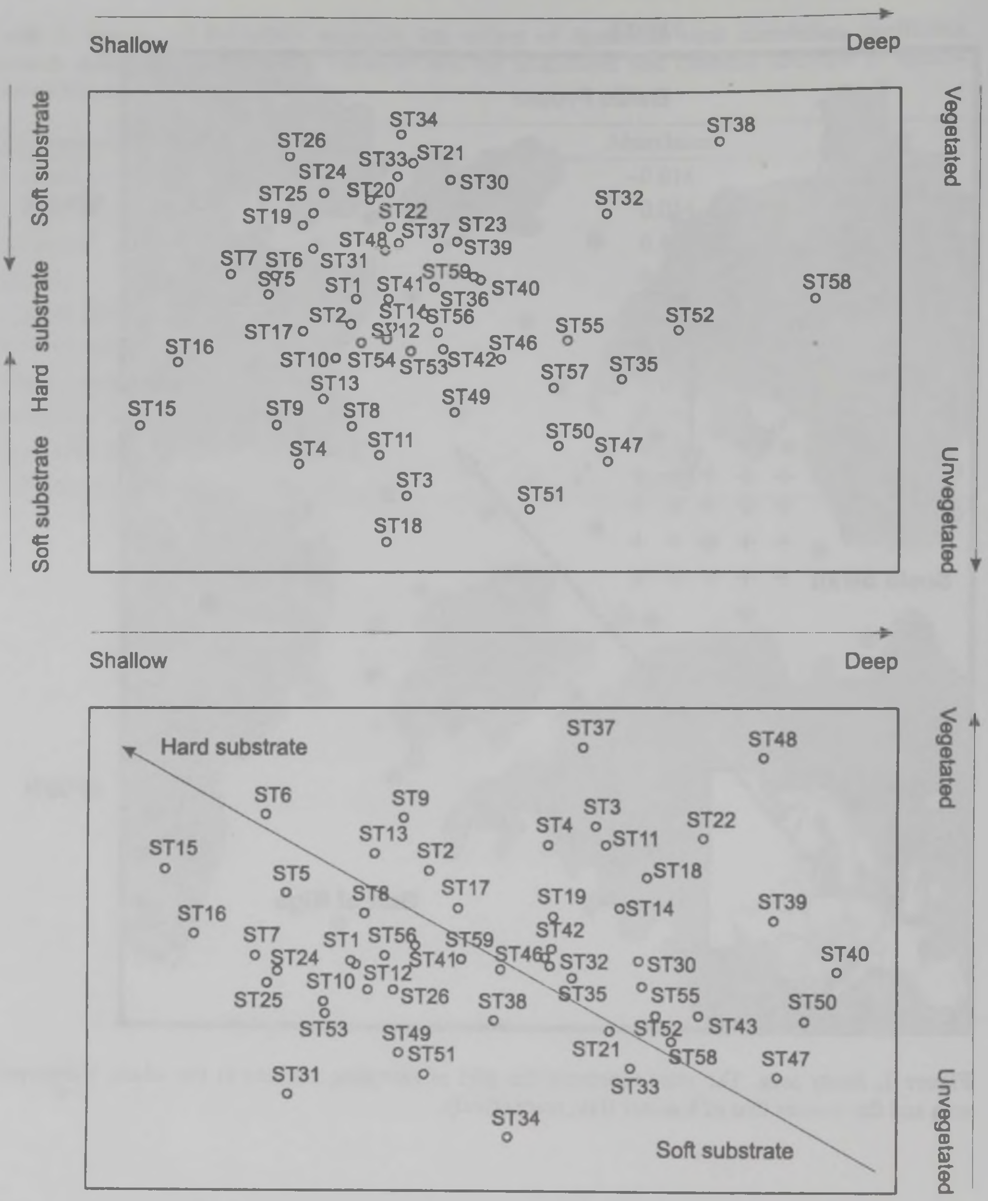

Figure 2. MDS ordination on the double square root transformed abundance (upper figure) and biomass (lower figure) data of macrozoobenthos. Arrows indicate the gradients of the most important environmental factors.

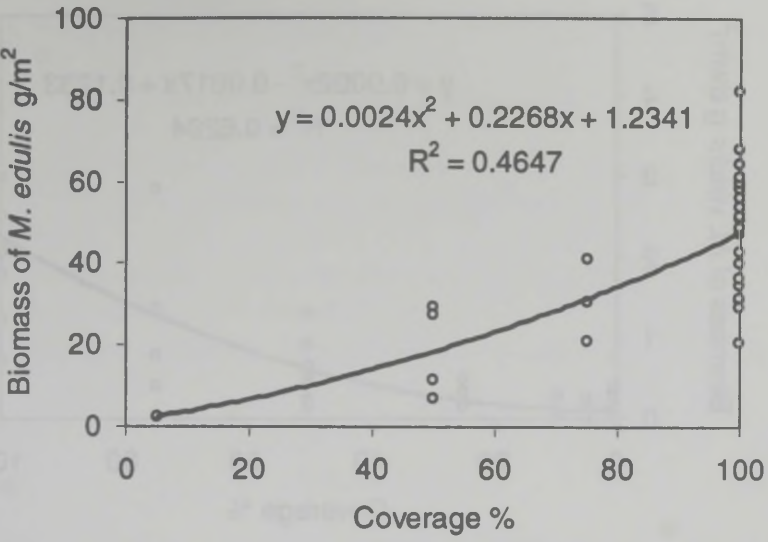

Figure 3. The relationship between the coverage of *F. lumbricalis* and the biomass of *M. edulis* in Kassari Bay in 1995.

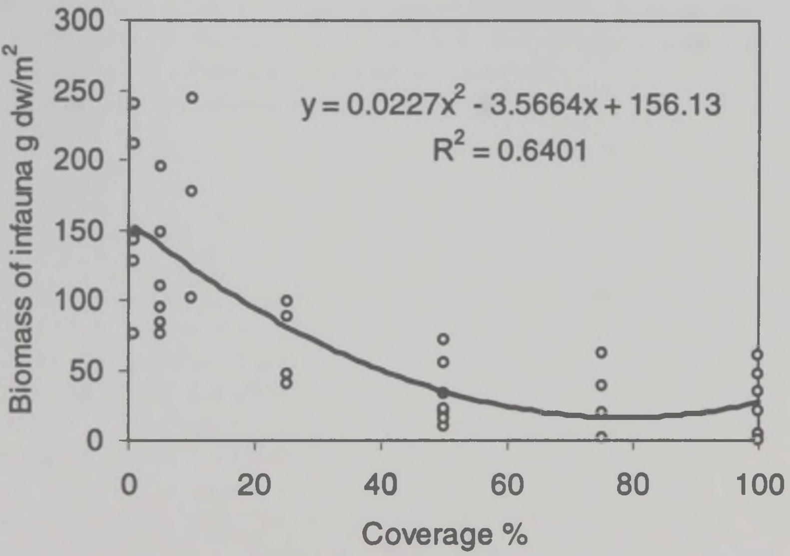

Figure 4. The relationship between the coverage of *F. lumbricalis* and the biomass of infauna in Kassari Bay in 1995.

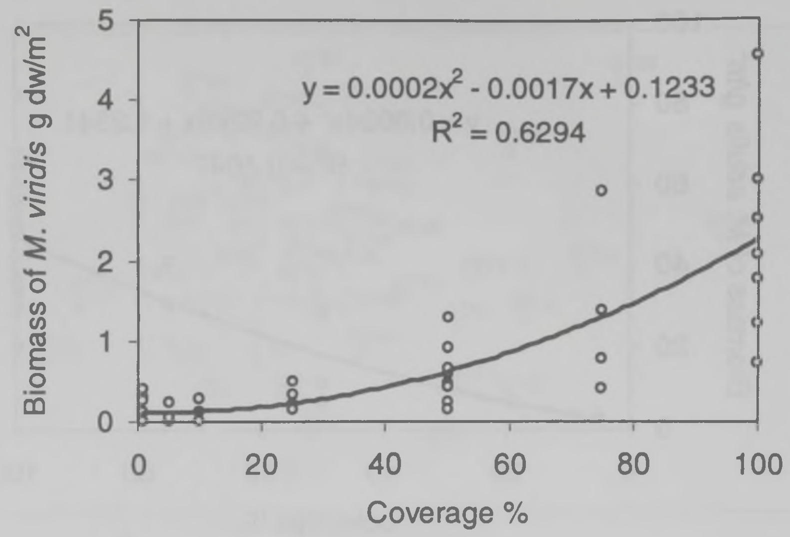

Figure 5. The relationship between the coverage of *F. lumbricalis* and the biomass of *M. viridis* in Kassari Bay in 1995.

VII

Kotta, J. & Rissanen, J.
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;

KOTTA and KOTTA, 1995). 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* Bruguière).

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., *Gammarus* 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 (*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 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 (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, KAUTSKY *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.

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7. REFERENCES

BEGON, M., J. L. HARPER and C. R. TOWNSEND, 1996: Ecology. Individuals, populations and communities. — Blackwell Science, Oxford, 1088 pp.

BERZINSH, V., 1995: Hydrological regime. — *In*: OJAVEER, E. (Ed.): Ecosystem of the Gulf of Riga between 1920 and 1990. Academia 5. pp. 7–31. Estonian Academy Publishers.

CLARKE, K. R., 1993: Non-parametric multivariate analyses of changes in community structure. — Aust. J. Ecol. **18**: 117–143.

CLARKE, K. R. and R. H. Green, 1988: Statistical design and analysis for a 'biological effects' study. — Mar. Ecol. Prog. Ser. **46**: 213–226.

CLARKE, K. R. and R. M. WARWICK, 1994: Changes in marine communities: an approach to statistical analysis and interpretation. — Plymouth Marine Laboratory, UK, 144 pp.

ELMGREN, R. and B. GANNING: 1974: Ecological studies of two shallow brackish water ecosystem. — Contrib. Askö Lab. Univ. Stockholm, Sweden **6**: 1–56.

HELCOM, 1993: First assessment of the state of the coastal waters of the Baltic Sea. — Balt. Sea. Environ. Proc. **54**: 1–160.

HISCOCK, K. and R. HOARE, 1973: A portable suction sampler for rock epibiota. — Helgol. Meeresunters. **25**: 35–38.

JÄRVEKÜLG, A., 1961: Mõnede bentiliste ja nektobentiliste selgrootute levikust Riia lahe kirdeosas. — Eesti NSV TA Toimetised Biol. **10**: 214–230.

JÄRVEKÜLG, A., 1962: Põhjaloomastiku varudest Riia lahe kirdeosas. — Kalatööstus, Tallinn **1**: 48–52.

JÄRVEKÜLG, A., 1979: Benthic fauna in the eastern part of the Baltic Sea. — Valgus, Tallinn, 384 pp (in Russian).

KANGAS, P., 1972: Quantitative sampling equipment for the littoral benthos. II. — IBP i Norden **10**: 9–16.

KAUTSKY, H., G. MARTIN, A. MÄKINEN, M. BORGIEL, P. VAHTERI and J. RISSANEN, 1999: Structure of phytobenthic and associated animal communities in the Gulf of Riga. — Hydrobiologia **393**: 191–200.

KOTTA, I. and J. KOTTA, 1997: 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. — *In*: OJAVEER, E. (Ed.): Proceedings of the 14th Baltic Marine Biologists Symposium. pp. 70–79. Estonian Academy Publishers.

KOTTA, J. and I. KOTTA, 1995: The state of macrobenthos of Pärnu Bay in 1991 as compared to 1959–1960. — Proc. Est. Acad. Sci. Ecol. **5**: 26–37.

KOTTA, J. and I. KOTTA, 1997: Do the towns of Helsinki and Tallinn oppress the zoobenthos in the adjacent sea? — Est. Mar. Inst. Rep. Ser. **8**: 55–71.

LAGZDINSH, G. S., 1975: Benthic fauna in the Gulf of Riga as the indicator of pollution. — *In*: VIRBITSKAS, YU., R. KROTAS and I. MANYUKAS (Eds.): Fundamentals of bioproductivity of the inner water bodies of the Baltic region. Proceedings of XVIII scientific conference of the research of the inner waterbodies of the Baltic States. pp. 429–430. Institute of Zoology and Parasitology, Academy of Sciences of Lithuanian SSR (in Russian).

LEPPÄKOSKI, E., 1975: Assessment of degree of pollution on the basis of macrozoobenthos in marine and brackish-water environments. — Acta Acad. Aboensis. Ser. B Math. et Phys. **35**: 1–90.

OJAVEER, H., 1997: Composition and dynamics of fish stocks in the Gulf of Riga ecosystem. — Dissertationes Biologicae Universitatis Tartuensis **31**: 1–138.

ORAV, H. and J. KOTTA, 2000: Factors affecting the distribution of benthic invertebrates in the phytal zone of the north-easten Baltic Sea. — Proc. Est. Acad. Sci. Biol. Ecol. **49**: 253–269.

SHURIN, A. T., 1953: Benthic fauna of the Gulf of Riga. — Tr. Latv. Odteleniya VNIRO **1**: 77–113 (in Russian).

SHURIN, A. T., 1960: Benthic fauna of the Gulf of Riga and its dispersion patterns. — Tr. VNIRO **42**: 37–60 (in Russian).

SHURIN, A. T., 1961: Assemblages of benthic fauna in the Gulf of Riga. — Tr. NIIRH SNH Latv. SSR **3**: 343–368 (in Russian).

SKULT, P., 1977: Composition of phytal macrofauna communities on transects extending seawards from Helsinki. — Mem. Soc. Fauna Flora Fenn. **53**: 43–56.

SOKAL, R. R. and F. J. ROHLF, 1981: Biometry. The principles and practice of statistics in biological research. — W.H. Freeman, San Francisco, California, 859 pp.

STÅLNACKE, P., N. VAGSTAD, T. TAMMINEN, P. WASSMANN, V. JANSONS and E. LOIGU, 1999: Nutrient runoff and transfer from land and rivers to the Gulf of Riga. — Hydrobiologia **410**: 103–110.

SUURSAAR, Ü., 1995: Nutrients in the Gulf of Riga. *In*: OJAVEER, E. (Ed.): Ecosystem of the Gulf of Riga between 1920 and 1990. Academia 5. pp. 41–50. Estonian Academy Publishers.

TENSON, J., 1995: Phytoplankton of the Pärnu Bay. — *In*: OJAVEER, E. (Ed.): Ecosystem of the Gulf of Riga between 1920 and 1990. Academia 5. pp. 105–126. Estonian Academy Publishers.

WASSMANN, P., 1996: Pelagic eutrophication and sediment. Final data report for field work carried out between 1993–1995. Nordisk Miljøforskningsprogram, Miljøforskningssamarbeid i Østersjøområdet (mimeo).

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

Model	Total	Filter-feeder	Herbivore	Carnivore	Detrivore	Omnivore
Sediment						
Abundance	**<0.001**	0.069	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Biomass	0.573	0.809	**<0.001**	0.988	0.209	**<0.001**
Vegetation						
Abundance	**0.025**	**0.001**	**<0.001**	0.202	0.660	**<0.001**
Biomass	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.170	**<0.001**

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 $p<0.05$

Region	A	B	C	D
Abundance				
B	**0.02**			
C	**0.02**	0.20		
D	**0.01**	**0.02**	0.64	
E	**0.02**	**0.01**	0.45	0.24
Biomass				
B	0.68			
C	**0.03**	**0.02**		
D	0.12	**0.02**	0.50	
E	**0.03**	**0.01**	**0.02**	0.12

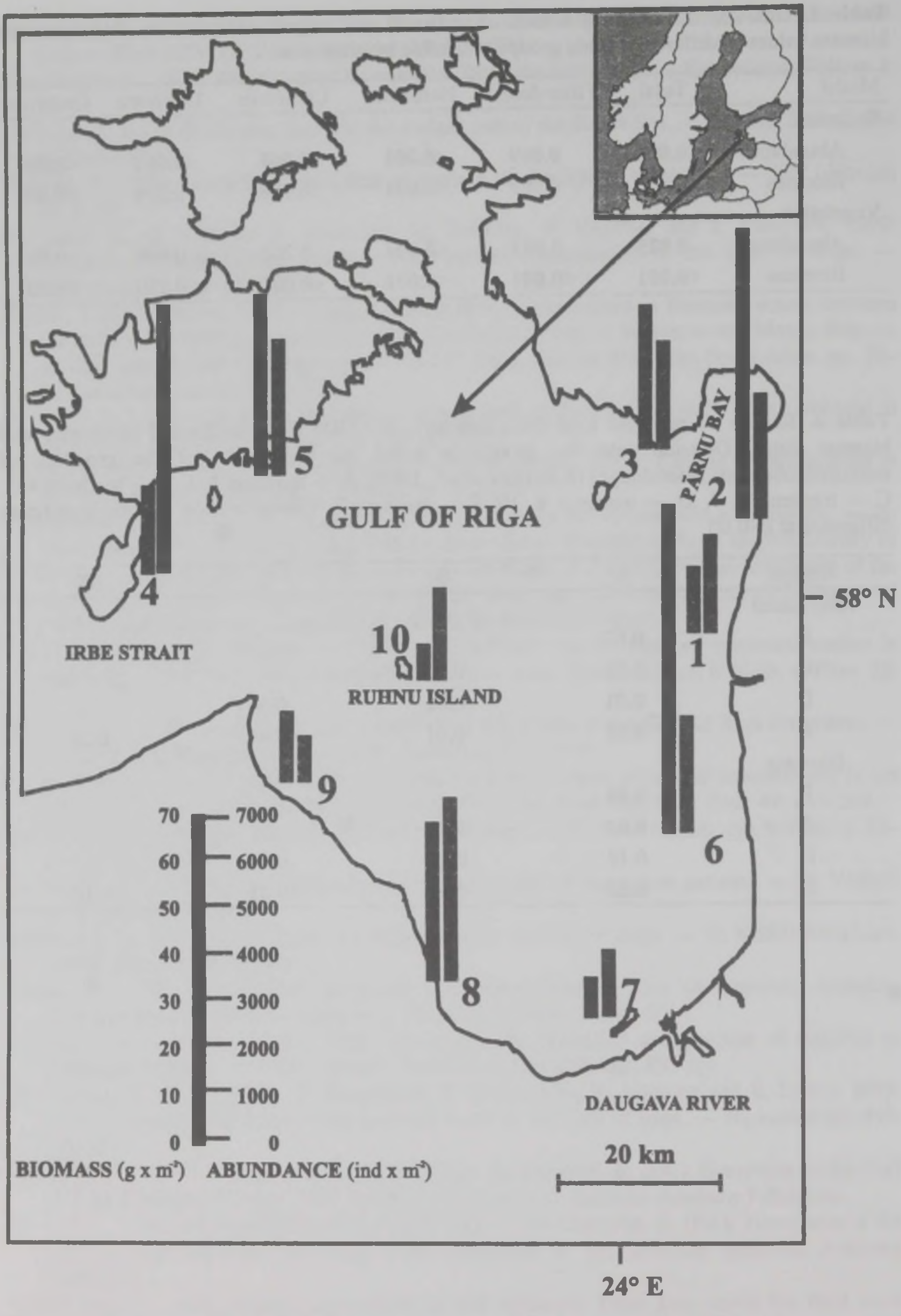

Figure 1. Study area. Numbers indicate the location of the transects. The left bar shows average biomass, the right bar average abundance of macrozoobenthos in the transect.

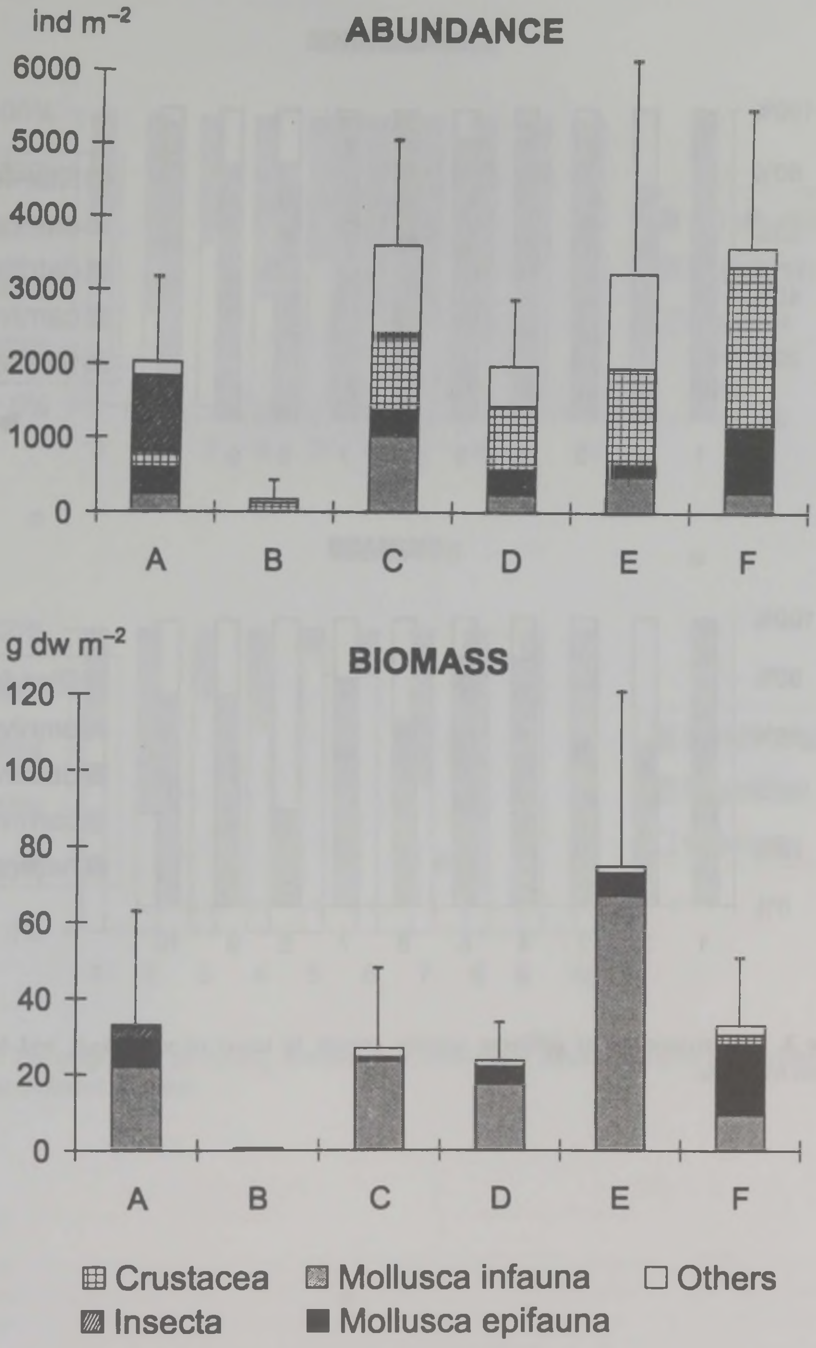

Figure 2. Average abundance and biomass values of different taxonomic groups of macrofauna with 95% confidence intervals in shallow water vascular plant communities (*n*=18) (A), shallow (< 1 m) unvegetated sandy bottoms at the south-eastern (*n*=9) (B) and north-western coast (*n*=12) (C), unvegetated 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).

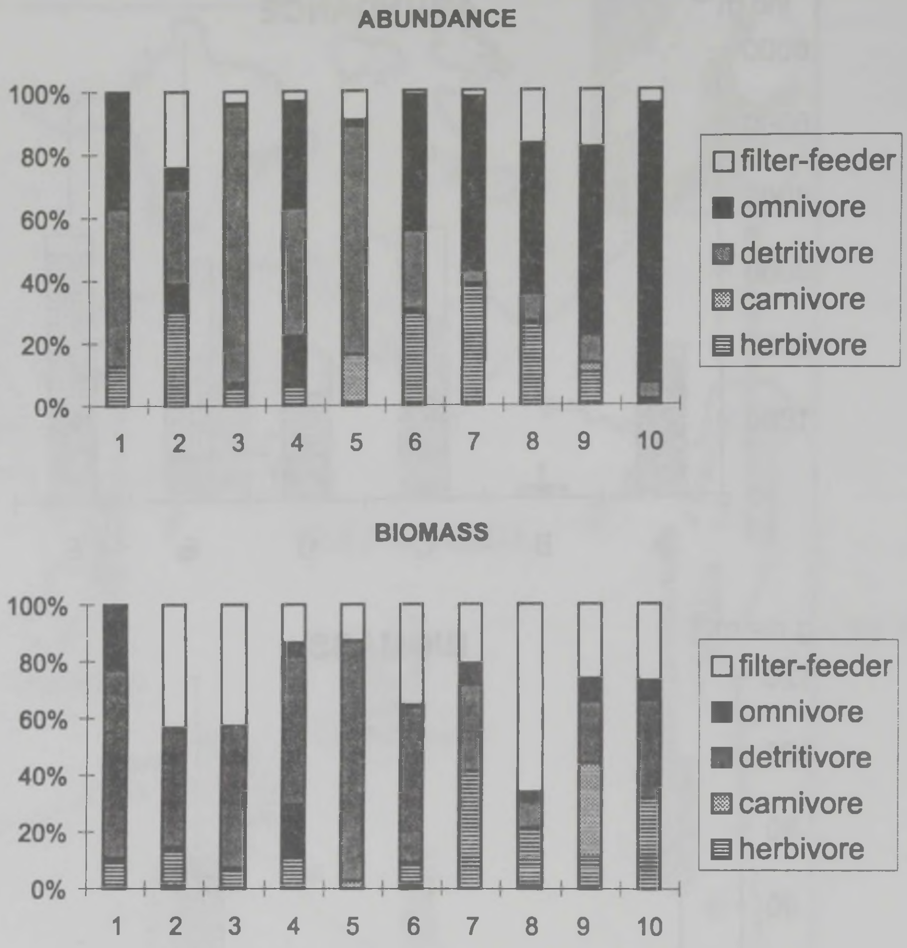

Figure 3. The proportion of different trophic groups in terms of abundance and biomass at different transects.

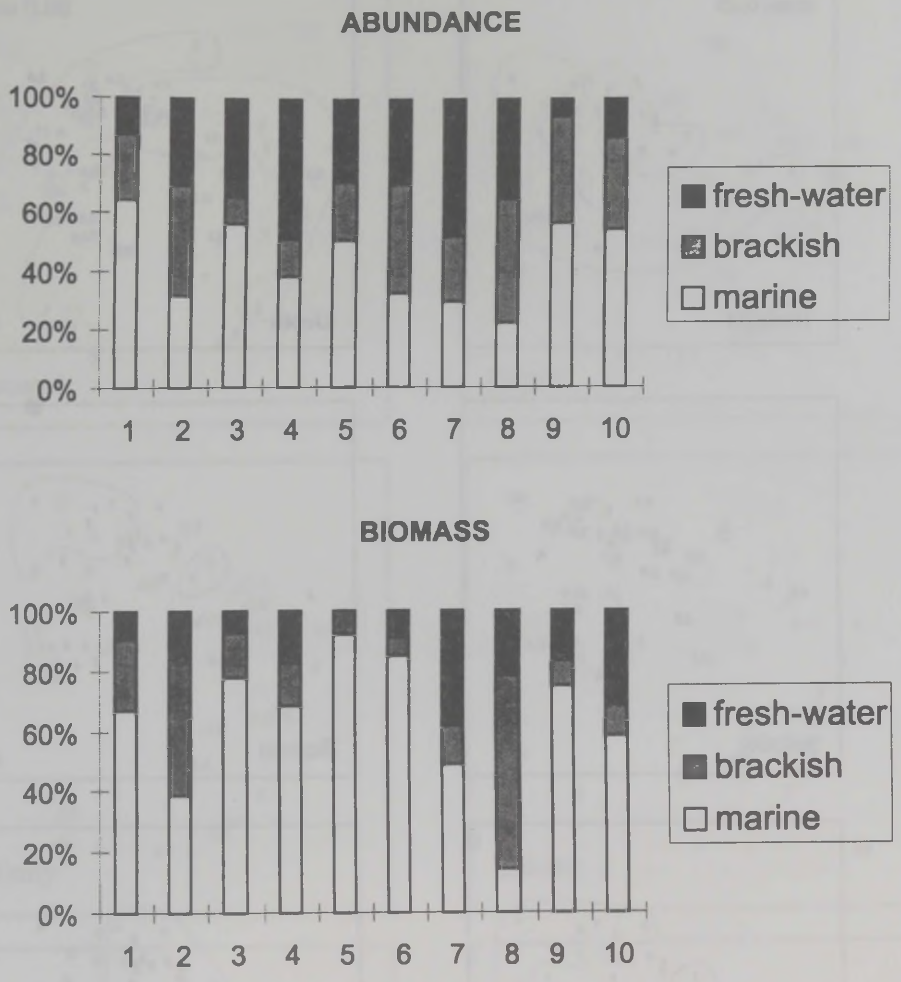

Figure 4. The proportion of marine, brackish and fresh-water species in terms of abundance and biomass at different transects.

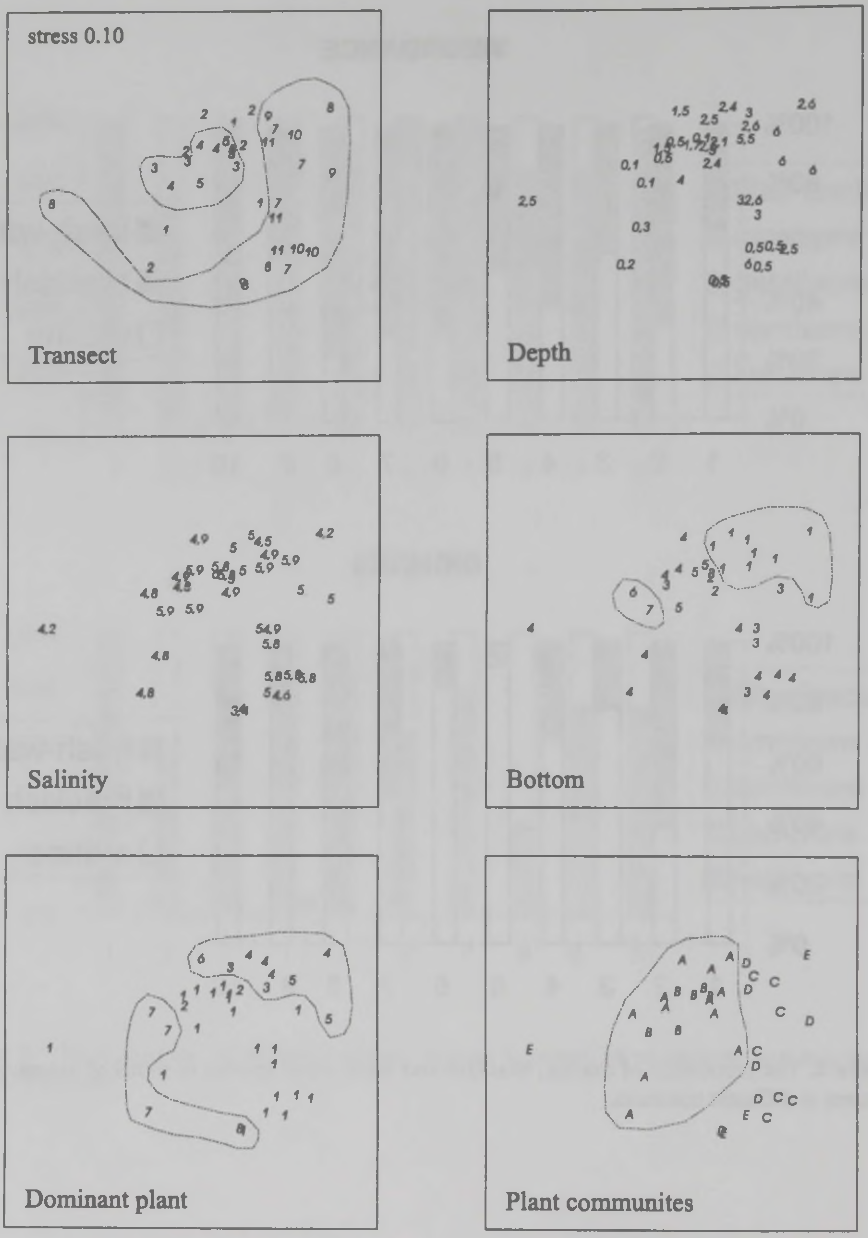

Figure 5. MDS ordination of sampling sites based on macrozoobenthos log-transformed abundance. On the ordination of study sites the number of transects, depth, salinity, bottom type, dominant plant species and type of plant communities are extrapolated. Bottom types are: 1 — stone, 2 — sandy gravel, 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.

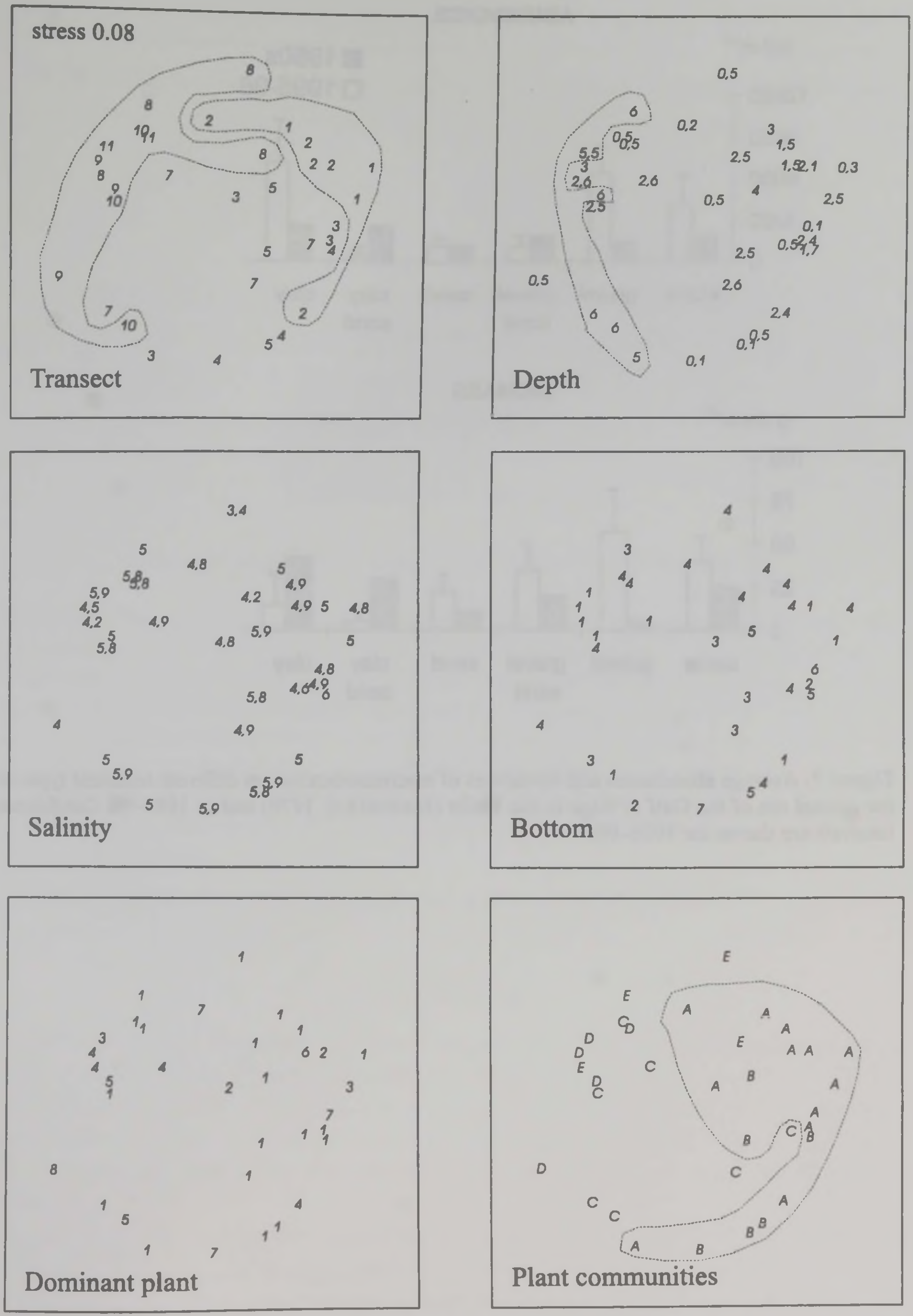

Figure 6. MDS ordination of sampling sites based on macrozoobenthos log-transformed biomass. For further explanation see Fig. 5.

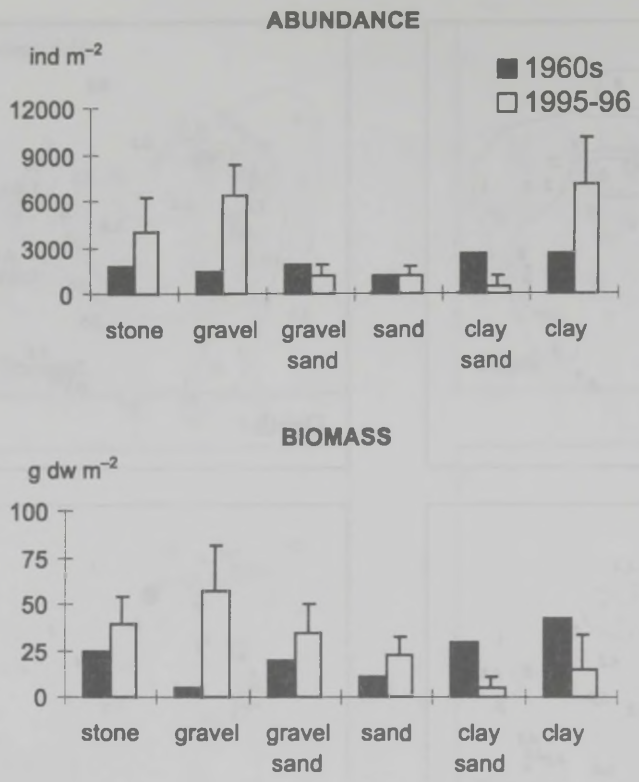

Figure 7. Average abundances and biomasses of macrozoobenthos on different sediment types in the coastal sea of the Gulf of Riga in the 1960s (JÄRVEKÜLG, 1979) and in 1995–96. Confidence intervals are shown for 1995–96.

VIII

Kotta, I. & Kotta, J. 1997.
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.
In *Proc. 14th Baltic Mar. Biol. Symp.* (Ojaveer, E., ed.).
Estonian Academy Publishers, Tallinn, 70–79.

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 commmunities 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).

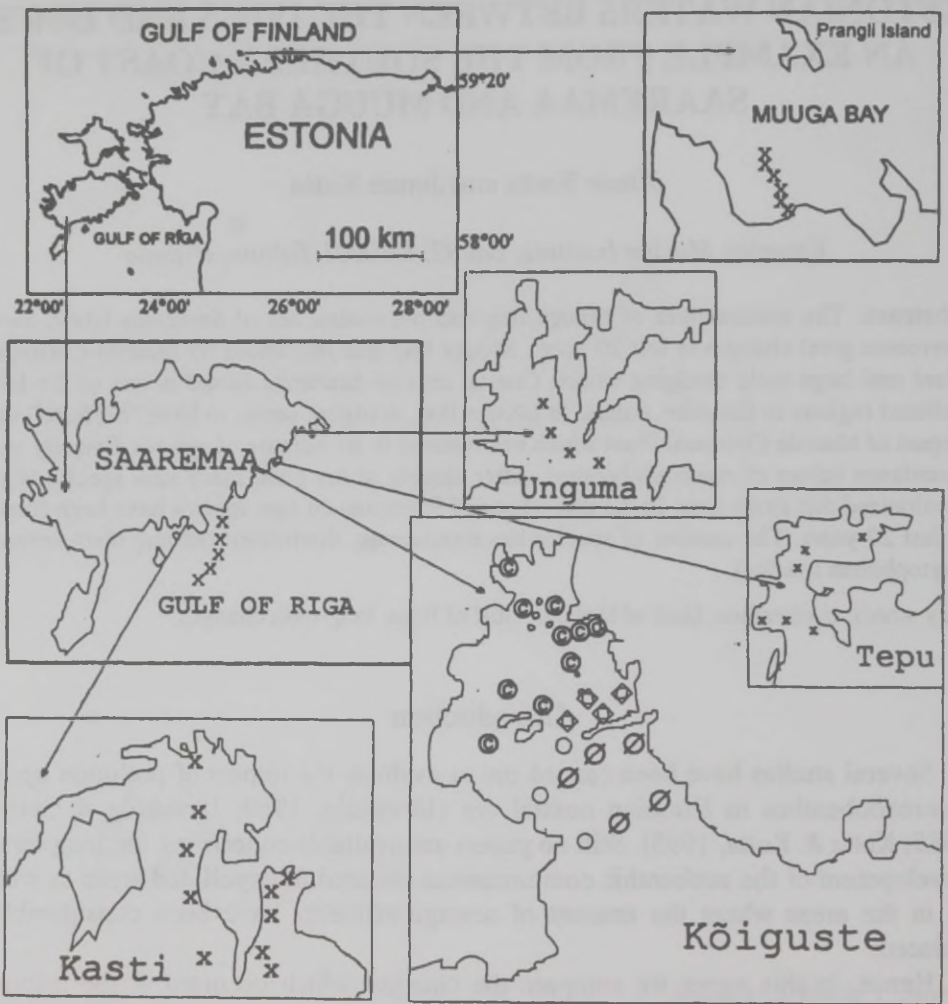

Figure 1. Study area; x, ◇, Ø, ○, © - sampling stations ◇-dredging areas; Ø - accumulation areas; Ø, ○ - open areas; © - closed areas.

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 m^2, 25 kg) was used for sampling in Muuga Bay and a modified Petersen bottom grab (0.0172 m^2, 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

Statistical differences (two-way ANOVA) between year, sediment type and study site in the biomass, abundance and species number of macrozoobenthos in the coastal sea of Saaremaa

Model	*Factor*			*Covariate*
	Year	*Sediment type*	*Interaction*	*Depth*
1. Biomass	0.5105	0.0730	0.5602	0.3828
2. Abundance	0.1706	0.6451	0.2477	0.2477
3. Sp. number	**0.0063**	**0.0051**	0.0974	0.0823
	Year	*Study site*	*Interaction*	*Depth*
4. Biomass	0.7337	**0.0038**	0.9388	0.1307
5. Abundance	0.3197	**0.0173**	0.8482	0.1582
6. Sp. number	**0.0000**	**0.0139**	0.5023	**0.0101**

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).

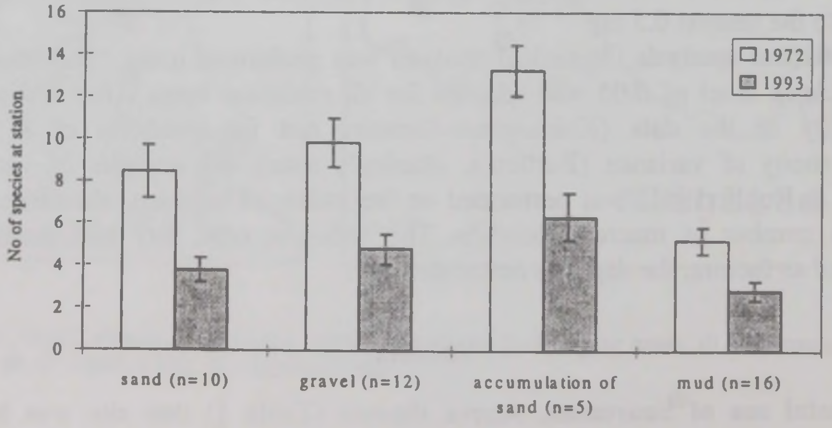

Figure 2. Mean values of number of species, with 95% confidence intervals, at different sediment types of the coastal sea of Saaremaa in 1972 and 1993.

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.), *Oligichaeta spp.* and *Chironomidae larvae*.

In the beginning of the 80's very dense populations of four species – *M. balthica, N. diversicolor, Mytilus 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.*

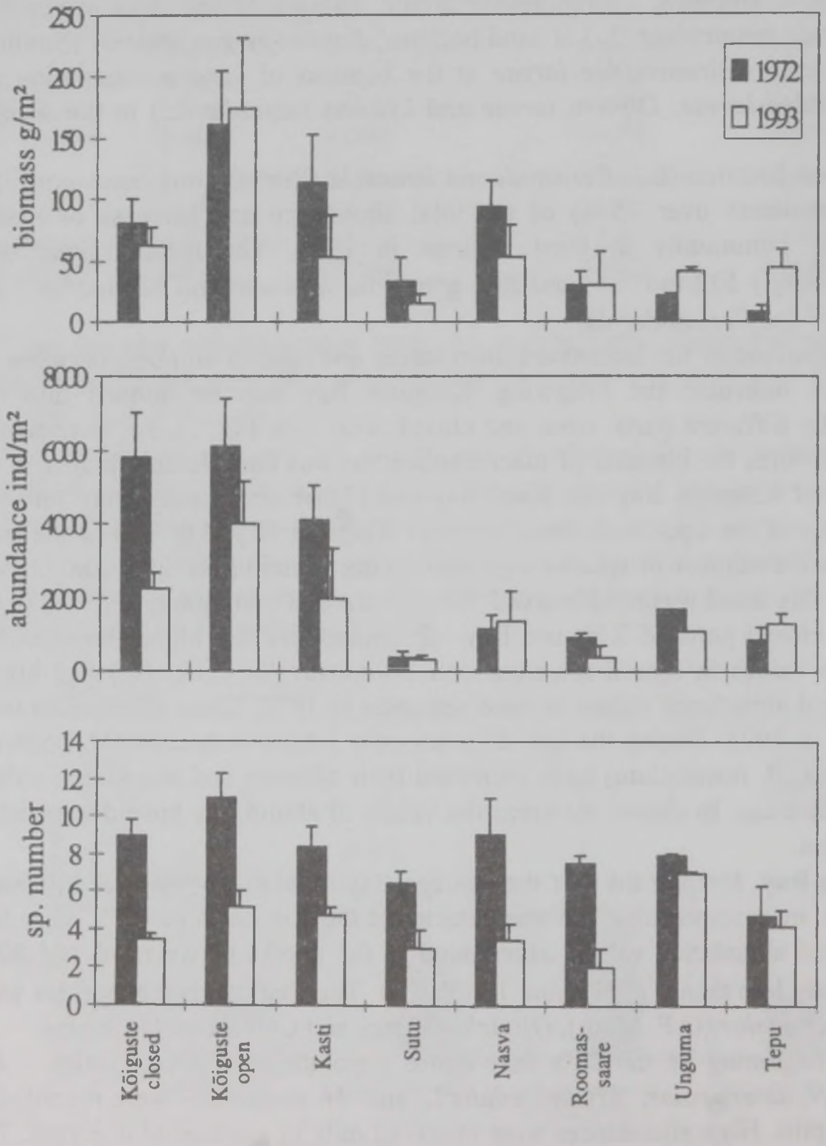

Figure 3. Mean values of biomass, abundance and species number of macrozoobenthos with 95% confidence intervals in the coastal sea of Saaremaa in 1972 and 1993.

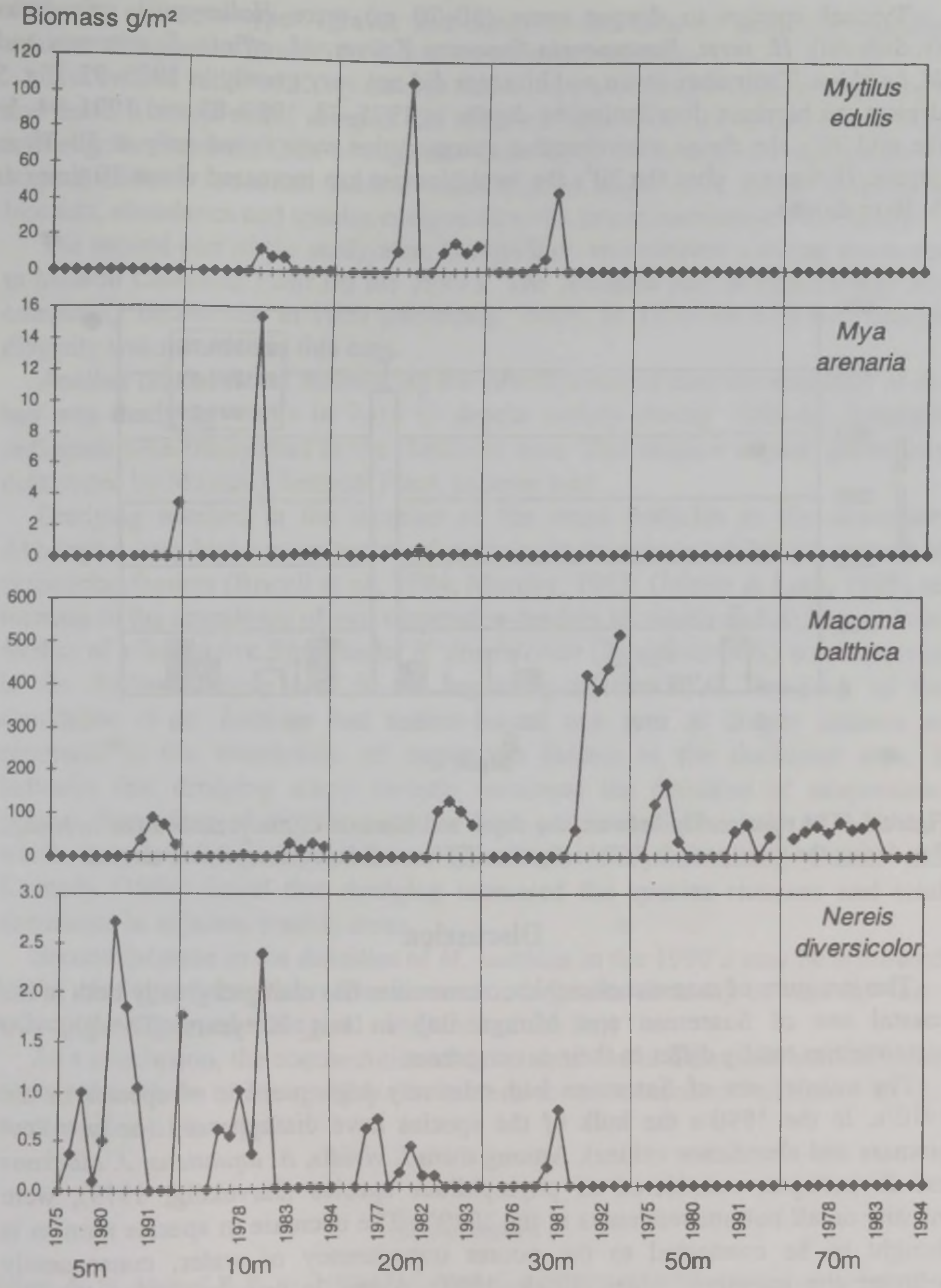

Figure 4. Biomass of *Mytilus edulis*, *Mya arenaria*, *Macoma balthica* and *Nereis diversicolor* in Muuga Bay in 1975–1994.

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.

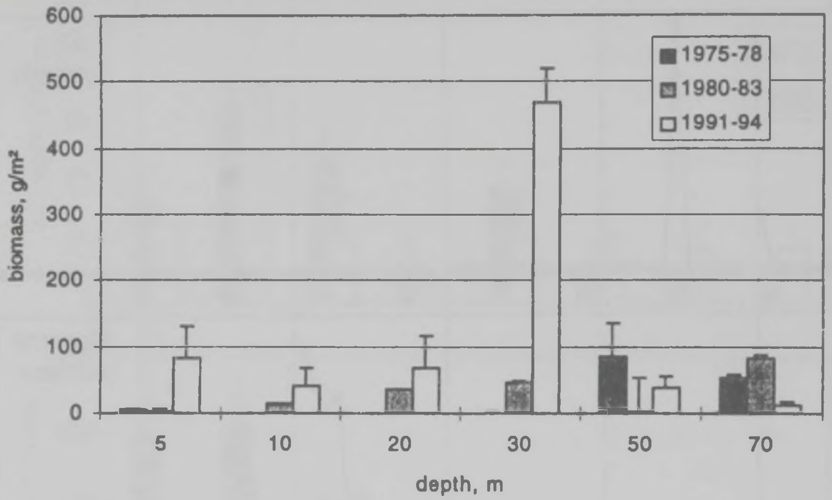

Figure 5. The relationship between the depth and biomass of macrozoobenthos in Muuga Bay during the three periods of investigation (95% confidence intervals are shown).

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). Similarily 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

Bricelj, V. M., Malouf, R.,E., de Quillfeldt, C. 1984. Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. Mar. Biol. 84: 167–173.

Grizzle, R. E. & Lutz, R. A. 1989. A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. Mar. Biol. 102: 95–105.

Hummel, H. 1985. Food intake of *Macoma balthica* (*Mollusca*) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 19: 52–76.

Järvekülg, A. 1969. The influence of sewage water to the development of zoobenthos and capacity for self-purification in the bays of Baltic Sea. In: Andrušaitis, G.P., Katšalova, O.L., Kumsare, A.J., Laganovskaja, P.J., Leinerte, M.P., Matisone, M.N., Salna, L.J. (eds) XIV Conference of the water-bodies of inner Baltic Sea. Zinatne, p. 57–62 (in Russian).

Järvekülg, A. 1979. The benthic fauna of the eastern part of the Baltic Sea. Valgus. Tallinn. 382 p. (in Russian)

Järvekülg, A. & Seire, A. 1985. Long term changes in the bottom fauna of Tallinn Bay and their causes. In: T. Trei (ed.) Problems concerning bioindication of the ecological condition of the Gulf of Finland (Hydrobiological Researches XV), pp. 148–154. Academy of Sciences of the Estonian SSR, Institute of Zoology and Botany, Tallinn. 194 pp.

Kotta, J. & Kotta, I. 1995. The state of macrozoobenthos of Pärnu Bay in 1991 as compared to 1959–60. Proc. Estonian Acad. Sci. Ecol. 5, 1/2: 26–37.

Kukk, H. 1993. Floristic composition of the phytobenthos and its long-term changes in the Gulf of Riga, the Baltic Sea. Proc. Estonian Acad. Sci. Ecol. 3, 2: 85–91.

Murphy, R.C. 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon – the importance of bioturbation. J. mar. Res. 43: 673–692.

Poiner, I.R. & Kennedy, R. 1984. Complex pattern of change in the macrobenthos of a large sandbank following dredging. I. Community analysis. Mar. Biol. 78: 335–352.

Riisgård, H.U. 1991. Suspension feeding in the polychaete *Nereis diversicolor*. Mar. Ecol. Prog. Ser. 70: 29–37.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry. The principles and practice of statistics in biological research. Second edition. W. H. Freeman, San Fransisco, California, USA.

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Kotta, I., Kotta, J. 1997. 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. In: Ojaveer, E. (ed) Proceedings of the 14th Baltic Marine Biologists Symposium, Estonian Academy Publishers, Pärnu, Estonia, pp. 70–79.

Kotta, I., Kotta, J. 1999. Distribution and migration of mysids in the Gulf of Riga (Northern Baltic). Est. Acad. Sci. Biol. Ecol., 48, 4, 284–295.

Kotta, J. 2000. First record of the talitrid amphipod *Orchestia cavimana* in the northern Baltic Sea. Proc. Est. Acad. Sci. Biol. Ecol., 49, 2, 221–224.

Kotta, J., Kotta, I. 1995. The state of macrozoobenthos of Pärnu Bay in 1991 as compared to 1959–1960. Proc. Est. Acad. of Sci., Ecol., 5, 1/2, 26–37.

Kotta, J., Kotta, I. 1998. Distribution and invasion ecology of *Marenzelleria viridis* (Verrill) in the Estonian coastal waters. Proc. Est. Acad. Sci. Biol. Ecol., 47, 3, 210–217.

Kotta, J., Kotta, I., Kask, J. 1999. Benthic animal communities of exposed bays in the outermost part of the Gulf of Finland. Proc. Est. Acad. Sci. Biol. Ecol., 48, 2, 107–116.

Kotta, J., Kotta, I., Martin, G., Kukk, H. 1998. An overview about the published data of zoobenthos in the littoral part of the Gulf of Riga. Proc. Est. Acad. Sci. Biol. Ecol., 47, 2, 83–97.

Kotta, J., Kotta, I., Viitasalo, I. 2000. Effect of diffuse and point source nutrient supply on the low diverse macrozoobenthic communities of the northern Baltic Sea. Boreal Environ. Res., (in press).

Kotta, J., Orav, H., Kotta, I. 1998. Distribution and filtration activity of Zebra mussel, *Dreissena polymorpha* (Pallas) in the Gulf of Riga and the Gulf of Finland. Proc. Est. Acad. Sci. Biol. Ecol., 47, 1, 32–41.

Kotta, J., Paalme, T., Martin, G., Mäkinen, A. Major changes in macroalgae community composition affect the life history of *Idotea baltica*. Int. Rev. Hydrobiol., (in press).

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I., Lumberg, A. 1999. Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. ICES J. Mar. Sci., 56, 33–40.

Orav, H., Kotta, J., Martin, G. Factors affecting the distribution of benthic invertebrates in the phytal zone of the north-eastern part Baltic Sea. Proc. Est. Acad. Sci. Biol. Ecol., 3, 253–269.

Simm, M., Kotta, J. 2000. Changes in copper and cadmium content of male herring in relation to spawning. Proc. Est. Acad. Sci. Biol. Ecol., 4, (in press).

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Boucher, G., Kotta, J. 1996. Composition et diversité de la méiofaune du lagon de “Great Astrolabe Reef” (Fiji). In: Charpy, L., Charpy-Robaud, C., Newell P. (eds) The Great Astrolabe Reef Lagoon (Fiji): Results of the French-Fijian ASTRO Expedition. Meiofauna of soft Bottom Sediments in the Great Astrolabe Reef Lagoon. Oceanogr. Notes et Doc. 46, 47–52.

Kotta, I., Kotta, J. 1997. 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. In: Ojaveer, E. (ed) Proceedings of the 14th Baltic Marine Biologists Symposium, Estonian Academy Publishers, Pärnu, Estonia, pp. 70–79.

Kotta, I., Kotta, J. 1999. Distribution and migration of mysids in the Gulf of Riga (Northern Baltic). Est. Acad. Sci. Biol. Ecol., 48, 4, 284–295.

Kotta, J. 2000. First record of the talitrid amphipod *Orchestia cavimana* in the northern Baltic Sea. Proc. Est. Acad. Sci. Biol. Ecol., 49, 2, 221–224.

Kotta, J., Kotta, I. 1995. The state of macrozoobenthos of Pärnu Bay in 1991 as compared to 1959-1960. Proc. Est. Acad. of Sci., Ecol., 5, 1/2, 26–37.

Kotta, J., Kotta, I. 1998. Distribution and invasion ecology of *Marenzelleria viridis* (Verrill) in the Estonian coastal waters. Proc. Est. Acad. Sci. Biol. Ecol., 47, 3, 210–217.

Kotta, J., Kotta, I., Kask, J. 1999. Benthic animal communities of exposed bays in the outermost part of the Gulf of Finland. Proc. Est. Acad. Sci. Biol. Ecol., 48, 2, 107–116.

Kotta, J., Kotta, I., Martin, G., Kukk, H. 1998. An overview about the published data of zoobenthos in the littoral part of the Gulf of Riga. Proc. Est. Acad. Sci. Biol. Ecol., 47, 2, 83–97.

Kotta, J., Kotta, I., Viitasalo, I. 2000. Effect of diffuse and point source nutrient supply on the low diverse macrozoobenthic communities of the northern Baltic Sea. Boreal Environ. Res., (in press).

Kotta, J., Orav, H., Kotta, I. 1998. Distribution and filtration activity of Zebra mussel, *Dreissena polymorpha* (Pallas) in the Gulf of Riga and the Gulf of Finland. Proc. Est. Acad. Sci. Biol. Ecol., 47, 1, 32–41.

Kotta, J., Paalme, T., Martin, G., Mäkinen, A. Major changes in macroalgae community composition affect the life history of *Idotea baltica*. Int. Rev. Hydrobiol., (in press).

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I., Lumberg, A. 1999. Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. ICES J. Mar. Sci., 56, 33–40.

Orav, H., Kotta, J., Martin, G. Factors affecting the distribution of benthic invertebrates in the phytal zone of the north-eastern part Baltic Sea. Proc. Est. Acad. Sci. Biol. Ecol., 3, 253–269.

Simm, M., Kotta, J. 2000. Changes in copper and cadmium content of male herring in relation to spawning. Proc. Est. Acad. Sci. Biol. Ecol., 4, (in press).

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