

FACTORS AFFECTING THE DISTRIBUTION OF BENTHIC INVERTEBRATES IN THE PHYTAL ZONE OF THE NORTH-EASTERN BALTIC SEA

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Abstract. Macrozoobenthos was studied in the coastal sea of the north-eastern part of the Baltic Sea. Using permutation procedure the structure of macrozoobenthic assemblages was compared at 14 different phytobenthic assemblages and the contribution of different environmental factors to the variability in macrozoobenthos was computed. The transitions in macrozoobenthic assemblages between different vegetation types were gradual. Macrozoobenthos in *Fucus vesiculosus*, *Furcellaria lumbricalis*, *Pilayella littoralis*, and *Polysiphonia nigrescens* dominated assemblages differed significantly from other phytobenthic assemblages. As compared to abiotic variables biotic factors, e.g. the biomass structure of phytobenthos, described the structure of macrozoobenthic assemblages in the phytal zone better. Generally, *Chara* spp., *Pilayella littoralis*, and *Furcellaria lumbricalis* dominated assemblages were preferred by macrozoobenthos over other habitats and species with strong thalli over filamentous algae.

Key words: Baltic, distribution, macrozoobenthos, macrophytobenthos.

INTRODUCTION

Phytobenthic assemblages constitute a functionally important component of many marine and brackish water ecosystems (Petersen, 1918; Barnes & Hughes, 1988; Barnes, 1994; Kautsky, U., 1995) but they are often ignored during the surveys of invertebrate communities. Macrophyte beds usually support higher abundance of epibenthos and infauna than comparable unvegetated bottoms. This has been attributed to the higher sediment stability and habitat complexity, more diverse food resources, and lower predation pressure (Welsh, 1980; Barnes & Hughes, 1988; Wilson et al., 1990).

Invertebrate assemblages of the phytobenthic zone have been historically treated as the co-occurring species inhabiting a particular plant species

(Wojtusiak et al., 1984; Cyr & Downing, 1988a; Kautsky, H., 1995; Kurashov et al., 1996). However, in order to investigate plant–animal interactions it is necessary to clarify whether the distribution of invertebrate assemblages is plant specific. It is likely that benthic species are distributed in relation to an individual series of requirements rather than an undivided assemblage responding to a particular environmental gradient (Barnes & Hughes, 1988).

In the present study we sought relationships between abiotic environmental factors and biomass structure of phytobenthic and associated invertebrate assemblages in the north-eastern Baltic Sea. Owing to extensive coastal sea, diverse phytobenthic assemblages, and low physical and chemical gradients, the study area may be considered an ideal location for this type of investigation. Unlike the northern coast of the Baltic Sea (Kautsky, H., 1995) there is no clear depth induced zonality in sediment granulometry and phytobenthos species composition in the study area.

A total of 14 phytobenthic assemblages were investigated. Using permutation procedure we tested whether invertebrate assemblages were significantly different between different macrophytobenthic assemblages and which factors contributed most to the variability in benthic invertebrate assemblages. The main hypotheses were as follows: (1) Biotic factors contribute more than abiotic factors to the abundance and biomass structure of macrozoobenthos in the phytal zone; (2) Because of higher habitat complexity, macrozoobenthos in the algae of strong thalli clearly distinguishes from other phytobenthic assemblages.

MATERIAL AND METHODS

Study area

The study was carried out in the coastal waters of the West-Estonian Archipelago Sea, north-eastern Baltic Sea (Fig. 1). Owing to low salinity benthic assemblages are relatively poor in species and the share of brackish and fresh-water species is high in the area (Järvekülg, 1979; Kautsky, H., 1995; Kautsky et al., 1999).

The **Gulf of Riga** is a relatively isolated water body. Its average salinity varies from 0.5–2 PSU in surface layers of the southern districts to 7 PSU in the Irbe Strait. The northern part of the gulf is characterized by a wide coastal zone with a diverse bottom topography and extensive reaches of boulders. The southern part of the gulf, on the contrary, has a narrow coastal zone with sandy substrate down to a depth of 4 m. Boulders replace the sandy substrate at deeper areas (Berzinsh, 1995). Because of the considerable load of nutrients from the Daugava River, the nutrient concentrations of the Gulf of Riga are higher than those in the Väinameri Sea (Suursaar, 1995; Suursaar et al., 1998). Benthic vegetation is much poorer in the southern side than in the northern side of the gulf (Martin, 1999).

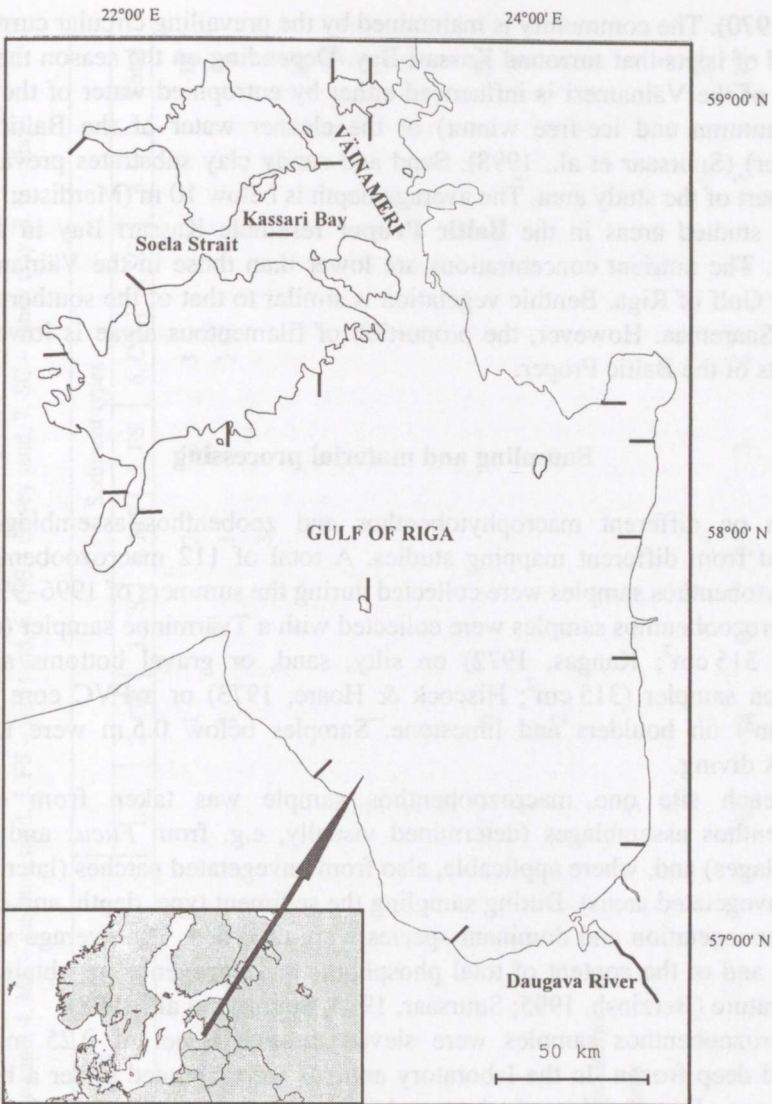


Fig. 1. Study area. Lines indicate the location of the transects.

According to hydrophysical properties, the **Väinameri** does not act as a single and unite water body in the water exchange processes (Suursaar et al., 1998). Kassari Bay is often separated by sub-fronts from the eastern part of the Väinameri and the Baltic Proper. The region is on average more “marine” (~7 PSU) than 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 *Furcellaria 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 Proper (summer) (Suursaar et al., 1998). Sand and sandy clay substrates prevail in the major part of the study area. The average depth is below 10 m (Mardiste, 1970).

The studied areas in the **Baltic Proper** resemble Kassari Bay in terms of salinity. The nutrient concentrations are lower than those in the Väinameri Sea and the Gulf of Riga. Benthic vegetation is similar to that of the southern coastal sea of Saaremaa. However, the proportion of filamentous algae is lower in the transects of the Baltic Proper.

Sampling and material processing

Data on different macrophytobenthos and zoobenthos assemblages were obtained from different mapping studies. A total of 112 macrozoobenthos and 336 phytobenthos samples were collected during the summers of 1996–99.

Macrozoobenthos samples were collected with a Tvärminne sampler (catching surface 315 cm²; Kangas, 1972) on silty, sand, or gravel bottoms and with a suction sampler (315 cm²; Hiscock & Hoare, 1973) or a PVC core sampler (175 cm²) on boulders and limestone. Samples below 0.5 m were taken by SCUBA diving.

In each site one macrozoobenthos sample was taken from different phytobenthos assemblages (determined visually, e.g. from *Fucus* and *Zostera* assemblages) and, where applicable, also from unvegetated patches (later referred to as unvegetated areas). During sampling the sediment type, depth, and coverage of macrovegetation and dominant species were recorded. The average values of salinity and of the content of total phosphorus and nitrogen were obtained from the literature (Berzinsh, 1995; Suursaar, 1995; Suursaar et al., 1998).

Macrozoobenthos samples were sieved through a net of 0.25 mm mesh size and deep frozen. In the laboratory animals were counted under a binocular microscope. Dry weights of plant and invertebrate species were obtained (to the nearest 0.1 mg) after drying the material at 60°C for 48 h. Molluscs were weighed with shells.

Table 1 shows the number of macrozoobenthos samples at different sediment types and phytobenthic assemblages. A phytobenthic assemblage was named according to plant species having the highest biomass (up to 3 species in case of no clear biomass domination) in the sample.

Additionally, three quantitative macrophytobenthos samples were taken by tossing frames (20 × 20 cm) haphazardly in each phytobenthos assemblage of each site. The samples were deep frozen and sorted, both plants and animals, to species level. The animals were counted. Each species was dried separately at 60°C for two weeks to allow larger plants to dry properly.

Table 1. The number of macrozoobenthos samples at different sediment types and phyto-benthic assemblages. The code of sediment is as follows: 1. S – stone, 2. GR – gravel, 3. CS – coarse sand, 4. MS – medium sand, 5. FS – fine sand, 6. CIS – clayey sand, 7. SC – sandy clay, 8. C – clay

Phyto-benthic assemblages	Sediment types								Total
	1. S	2. GR	3. CS	4. MS	5. FS	6. CIS	7. SC	8. C	
1. <i>Zannichellia palustris</i>		1		3	3	3			10
2. <i>Potamogeton pectinatus-Z. palustris-Zostera marina</i>		1		1		3			5
3. <i>Myriophyllum spicatum</i>				3					3
4. <i>Cladophora glomerata</i>	7		3						10
5. <i>Chara</i> spp.	1								1
6. <i>Pilayella littoralis</i>	3	1							4
7. <i>Sphacelaria arctica</i>	2								2
8. <i>Chorda filum</i>	2								2
9. <i>Fucus vesiculosus</i>	15	6							21
10. <i>Furcellaria lumbricalis</i>	4						1		5
11. <i>Polysiphonia nigrescens</i>		2							2
12. <i>S. arctica-C. glomerata-Ceramium tenuicorne</i>	3								3
13. <i>P. littoralis-P. nigrescens-F. lumbricalis</i>	5					1			6
14. <i>F. lumbricalis-S. arctica</i>	3								3
15. Unvegetated	45	18	11	21	3	6	1	7	112
Total									

Statistical procedure

The effect of sediment and vegetation types on the abundance or biomass of different invertebrate species was estimated by one-way analysis of variance (ANOVA or Kruskal–Wallis test) and multiple range test using least significant differences at $p < 0.05$ (Sokal & Rohlf, 1981).

Multivariate data analyses were performed by the statistical program PRIMER (Clarke & Warwick, 1994). Non-metric multidimensional scaling analysis (MDS) on double-square-root transformed data of invertebrate abundance or biomass was used to quantify the dissimilarities between invertebrate communities. Bray–Curtis similarity measure (Bray & Curtis, 1957) was used to construct the similarity matrices. The statistical differences in invertebrate assemblages between study regions were obtained by the ANOSIM permutation test (Clarke, 1993). The contribution of different taxa in the differences was calculated by the SIMPER procedure (Clarke, 1993). A Spearman rank correlation (ρ) was computed between the similarity matrices of invertebrate abundance or biomass and environmental data to examine the ecological significance of environmental variables in invertebrate assemblages (BIO–ENV procedure, Clarke & Ainsworth, 1993) and the significance of the correlation was determined by the PRIMER program RELATE (Clarke & Warwick, 1994). A permutation procedure is essential here because classical statistical approaches to significance testing are not valid for typical community matrices.

Depth, salinity, sediment type, and the content of total phosphorus and nitrogen in the water were involved as abiotic variables and the biomass of different plant species and the taxonomic, age, and morphological structure of phytobenthic assemblages as biotic variables. The variables describing taxonomic, age and morphological structure of phytobenthic assemblages were as follows: biomass of Rhodophyta, Phaeophyta, Chlorophyta, Charophyta, and Magnoliophyta; biomass of annual and perennial plants; and biomass of filamentous algae and algae with strong thalli.

RESULTS

A total of 38 benthic invertebrate and 26 plant species were observed in the study area. The species that had the highest biomass values in the study area are presented in Table 2. *Macoma balthica* and *Mytilus edulis* were most prevalent benthic invertebrate species and *Fucus vesiculosus* and *Furcellaria lumbicalis* most prevalent phytobenthic species through the studied depth gradient.

According to MDS analysis benthic invertebrate assemblages do not form clearly distinguished groups in terms of phytobenthic species (Fig. 2). Macrozoobenthos in *Myriophyllum spicatum*, *Chara aspera*, and *Fucus vesiculosus* was in sharp contrast (i.e. based on statistical distance, not necessarily statistically different) to other macroalgal species. Other transitions were more gradual. However, the variability of macrozoobenthic assemblages within a

Table 2. Dominant benthic plant and invertebrate species at different depth intervals in the study area

Depth, m	Plant	Invertebrate
<2	<i>Fucus vesiculosus</i>	<i>Lymnaea peregra</i>
	<i>Cladophora glomerata</i>	<i>Macoma balthica</i>
	<i>Pilayella littoralis</i>	<i>Mytilus edulis</i>
	<i>Enteromorpha intestinalis</i>	<i>Cerastoderma glaucum</i>
		<i>Theodoxus fluviatilis</i>
2-6	<i>Fucus vesiculosus</i>	<i>Mytilus edulis</i>
	<i>Furcellaria lumbricalis</i>	<i>Macoma balthica</i>
	<i>Pilayella littoralis</i>	<i>Mya arenaria</i>
	<i>Sphacelaria arctica</i>	<i>Dreissena polymorpha</i>
		<i>Theodoxus fluviatilis</i>
>6	<i>Furcellaria lumbricalis</i>	<i>Mytilus edulis</i>
	<i>Polysiphonia nigrescens</i>	<i>Macoma balthica</i>
	<i>Ceramium tenuicorne</i>	<i>Mya arenaria</i>
	<i>Sphacelaria arctica</i>	<i>Dreissena polymorpha</i>

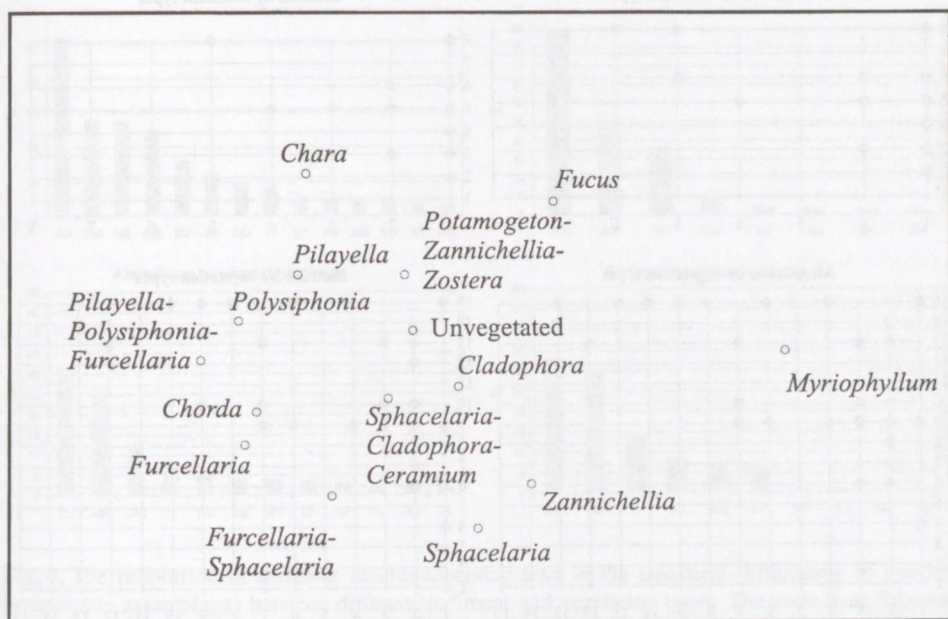


Fig. 2. Non-metric multidimensional scaling ordination of double square root macrozoobenthos biomass data by different phyto-benthic assemblages (stress 0.15).

particular phytobenthic species was relatively small and, hence, many differences were statistically significant (ANOSIM, $p < 0.05$; Fig. 3).

The abundance and biomass structure of invertebrate assemblages in *Fucus vesiculosus*, *Furcellaria lumbricalis*, and the mixed type of *Pilayella littoralis*, *Polysiphonia nigrescens*, and *Furcellaria lumbricalis* differed significantly from most other phytobenthic assemblages. Other differences were more erratic. Taking into account the sediment structure, stone bottoms clearly distinguished from other types in terms of both macrozoobenthos abundance and biomass. This reflects different phytobenthic species composition on stone bottoms as compared to other sediment types (see above the results of ANOSIM analysis and below those of BIO-ENV analysis).

To identify the environmental factors that are most strongly related to the variability of benthic invertebrate assemblages BIO-ENV analysis was run. The effect of environmental variables was similar on both the abundance and biomass structure of macrozoobenthos. Among abiotic variables salinity gave the best match with invertebrate assemblages in unvegetated areas (p equal to 0.323 and 0.183 for abundance and biomass, respectively) and sediment type in vegetated areas (0.365 and 0.285). The abundances and biomasses of *Cladophora glomerata* (0.427, 0.481), *Dictyosiphon foeniculaceus* (0.386, 0.313), *Enteromorpha intestinalis* (0.378, 0.427), Chlorophyta (0.428, 0.480), and annual

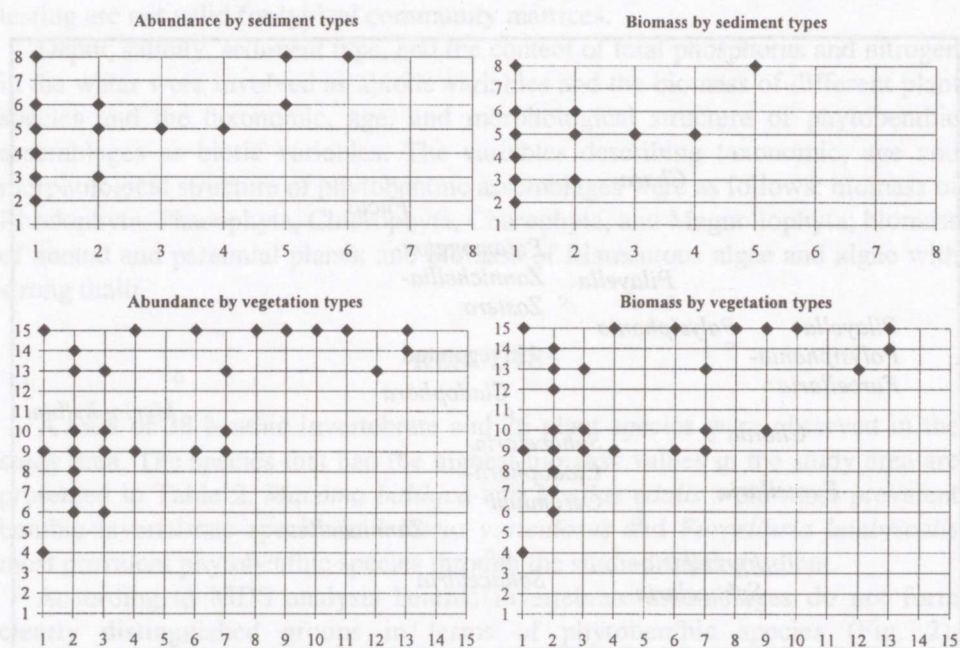


Fig. 3. The results of ANOSIM permutation tests. Dots indicate the presence of statistical differences ($p < 0.05$) in the abundance and biomass structure of macrozoobenthic assemblages between different sediment and vegetation types. For the code see Table 1.

plants (0.180, 0.196) were most important biotic variables in unvegetated areas and the biomass of *Zannichellia palustris* (0.423, 0.399), *Chara aspera* (0.410, 0.386), *Cladophora glomerata* (0.409, 0.389), *Urospora penicilliformis* (0.409, 0.391), *Tolypella nidifica* (0.408, 0.379), Charophyta (0.388, 0.330), and Magnoliophyta (0.314, 0.242) in vegetated areas.

Combining all environmental variables yielded only a slight increase in correlation coefficients. Salinity, *Cladophora glomerata*, *Dictyosiphon foeniculaceus*, and Chlorophyta showed the highest correlation with the abundance structure of benthic invertebrate assemblages (0.564); salinity, *Cladophora glomerata*, *Enteromorpha intestinalis*, and Chlorophyta with the biomass of benthic invertebrate assemblages (0.520) in unvegetated areas. In vegetated areas *Tolypella nidifica* and *Chara aspera* had the highest correlation with the abundance (0.461) and *Tolypella nidifica*, *Urospora penicilliformis*, and *Chara aspera* with the biomass structure of invertebrates (0.406). To conclude, the impact of biotic variables was superior over abiotic variables in explaining the variability in benthic invertebrate assemblages in the study area.

Macoma balthica, *Mytilus edulis*, *Cerastoderma glaucum*, *Lymnaea peregra*, *Theodoxus fluviatilis*, *Hydrobia ventrosa*, *Idotea viridis*, *Gammarus* spp., and *Nereis diversicolor* contributed most to the statistical differences in the above-mentioned multivariate analysis (Fig. 4). Figures 5 and 6 show the average

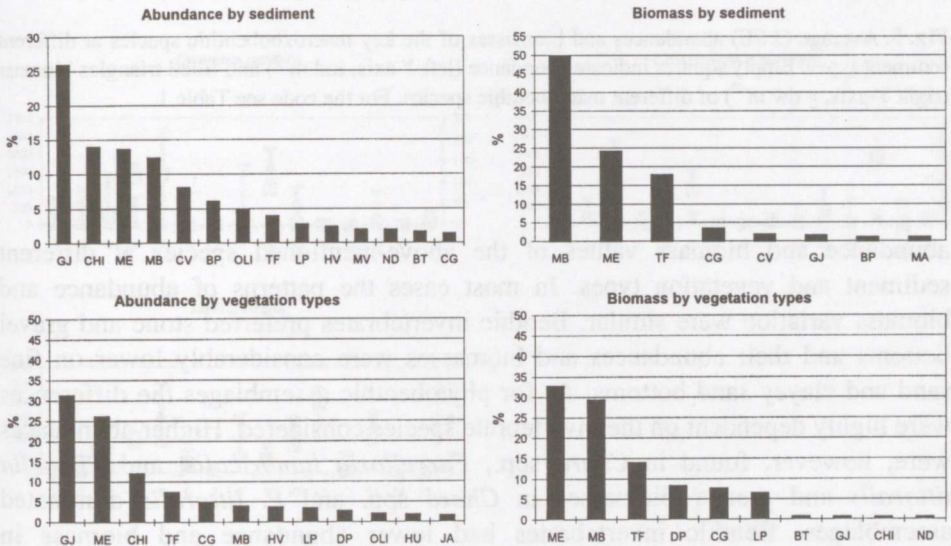


Fig. 4. The proportion of different macrozoobenthic taxa in the statistical differences of benthic invertebrate assemblages between different sediment and vegetation types. The code is as follows: MV – *Marenzelleria viridis*, ND – *Nereis diversicolor*, OLI – Oligochaeta, CHI – Chironomidae l., BP – *Bathyporeia pilosa*, CV – *Corophium volutator*, GJ – *Gammarus* juv., IV – *Idotea viridis*, BT – *Bithynia tentaculata*, CG – *Cerastoderma glaucum*, DP – *Dreissena polymorpha*, JA – *Jaera albifrons*, HV – *Hydrobia viridis*, HU – *Hydrobia ulvae*, LP – *Lymnaea peregra*, MB – *Macoma balthica*, MA – *Mya arenaria*, ME – *Mytilus edulis*, TF – *Theodoxus fluviatilis*.

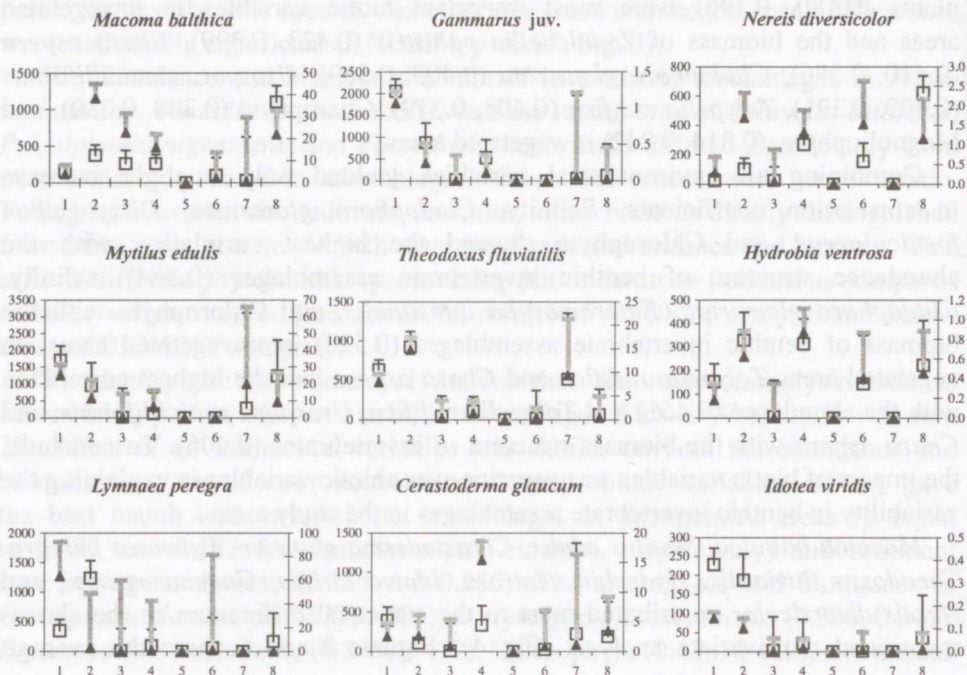


Fig. 5. Average (\pm SE) abundances and biomasses of the key macrozoobenthic species at different sediment types. Empty squares indicate abundance (left Y-axis, ind m⁻²) and filled triangles biomass (right Y-axis, g dw m⁻²) of different macrobenthic species. For the code see Table 1.

abundance and biomass values of the above-mentioned species at different sediment and vegetation types. In most cases the patterns of abundance and biomass variation were similar. Benthic invertebrates preferred stone and gravel bottoms and their abundances and biomasses were considerably lower on fine sand and clayey sand bottoms. As for phyto-benthic assemblages the differences were highly dependent on the invertebrate species considered. Higher abundances were, however, found in *Chara* spp., *Furcellaria lumbricalis*, and *Pilayella littoralis* and greater biomasses in *Chara* spp. and *P. littoralis* dominated assemblages. Benthic invertebrates had lower abundance and biomass in *Sphacelaria arctica* and *Zannichellia palustris* dominated assemblages.

Generally, annual and filamentous algae were least preferred by benthic invertebrates (Fig. 7). Nevertheless, these trends varied between species considered. *Macoma balthica* and *Cerastoderma glaucum* had highest biomass on annual algae and *Idotea* spp. and *Lymnaea peregra* highest abundance on

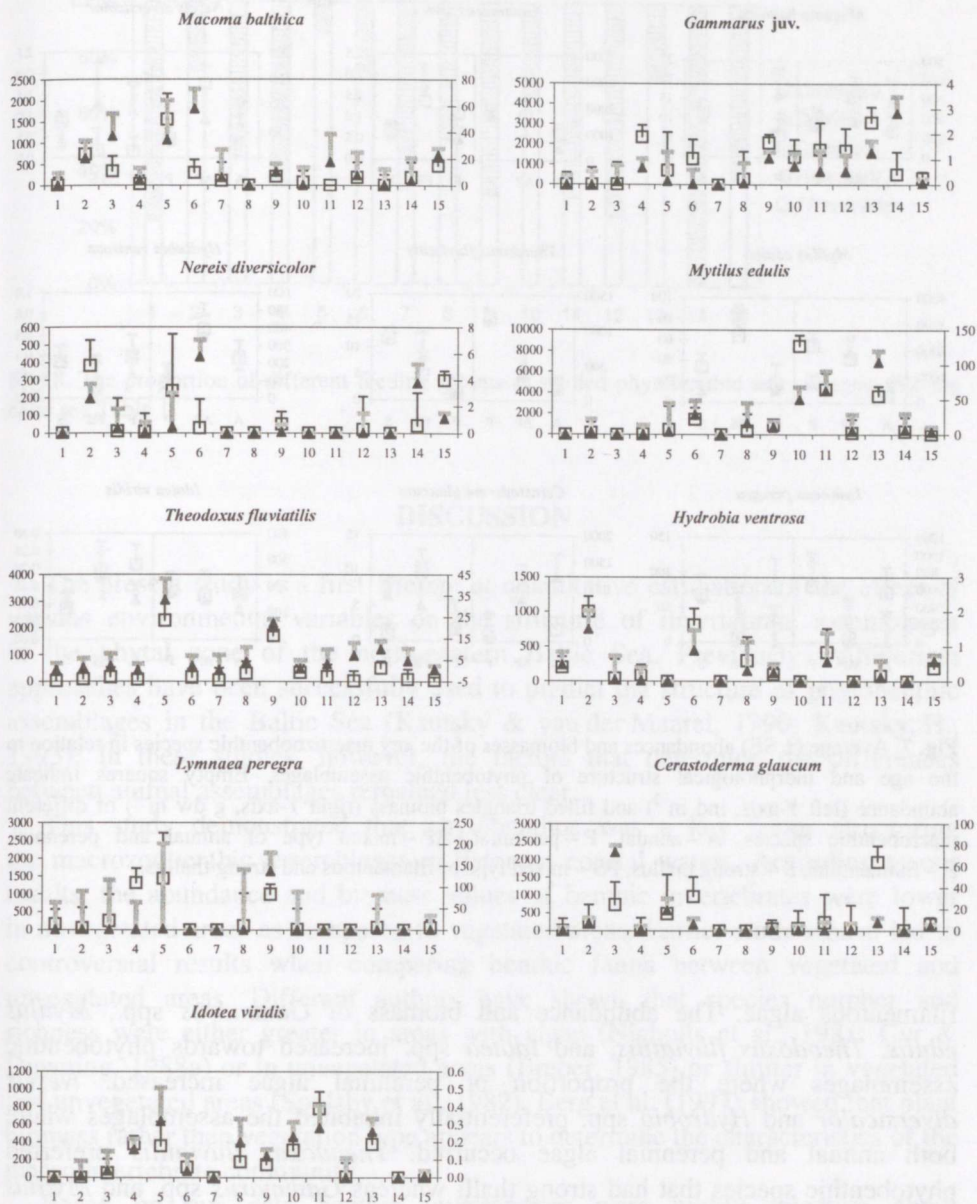


Fig. 6. Average (\pm SE) abundances and biomasses of the key macrozoobenthic species at different vegetation types. Empty squares indicate abundance (left Y-axis, ind m^{-2}) and filled triangles biomass (right Y-axis, g $dw m^{-2}$) of different macrobenthic species. For the code see Table 1.

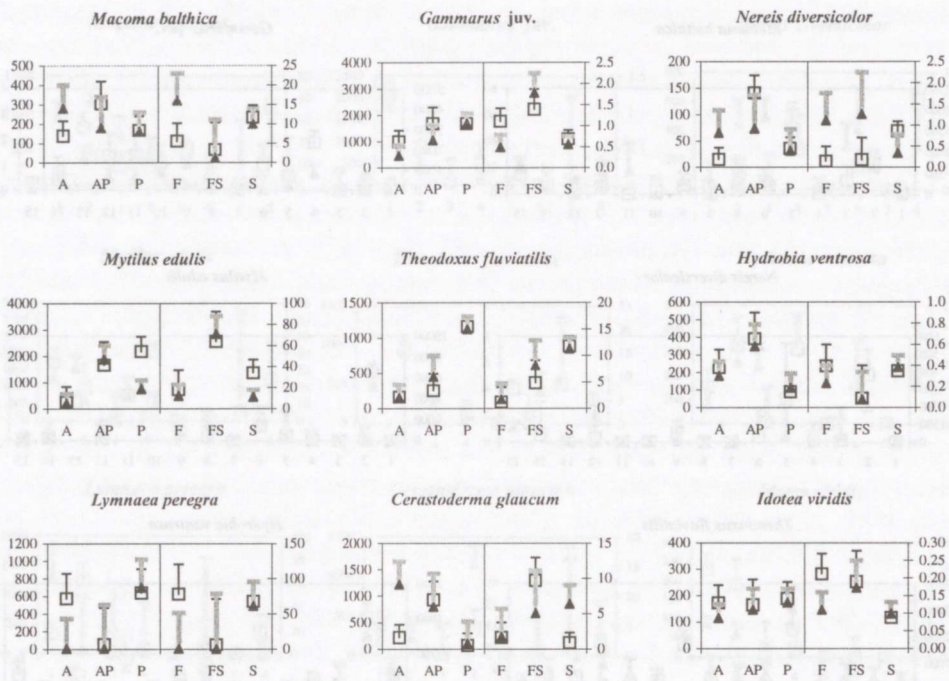


Fig. 7. Average (\pm SE) abundances and biomasses of the key macrozoobenthic species in relation to the age and morphological structure of phytobenthic assemblages. Empty squares indicate abundance (left Y-axis, ind m⁻²) and filled triangles biomass (right Y-axis, g dw m⁻²) of different macrobenthic species. A – annual, P – perennial, AP – mixed type of annual and perennial, F – filamentous, S – strong thallus, FS – mixed type of filamentous and strong thallus.

filamentous algae. The abundance and biomass of *Gammarus* spp., *Mytilus edulis*, *Theodoxus fluviatilis*, and *Idotea* spp. increased towards phytobenthic assemblages where the proportion of perennial algae increased. *Nereis diversicolor* and *Hydrobia* spp. preferentially inhabited the assemblages where both annual and perennial algae occurred. *Theodoxus fluviatilis* preferred phytobenthic species that had strong thalli whereas *Gammarus* spp. and *Mytilus edulis* preferred mixed assemblages of filamentous and strong thallus species.

As to the trophic composition of invertebrate assemblages, the proportion of herbivores was the highest in *Zannichellia palustris*, *Chara* spp., and *Fucus vesiculosus*; that of filter-feeders in *Furcellaria lumbricalis*, *Chorda filum*, and *Sphacelaria arctica*; detritivores in *Pilayella littoralis*, *Potamogeton pectinatus*–*Zannichellia palustris*–*Zostera marina*, and unvegetated areas; and omnivores in *Furcellaria lumbricalis* dominated assemblages (Fig. 8).

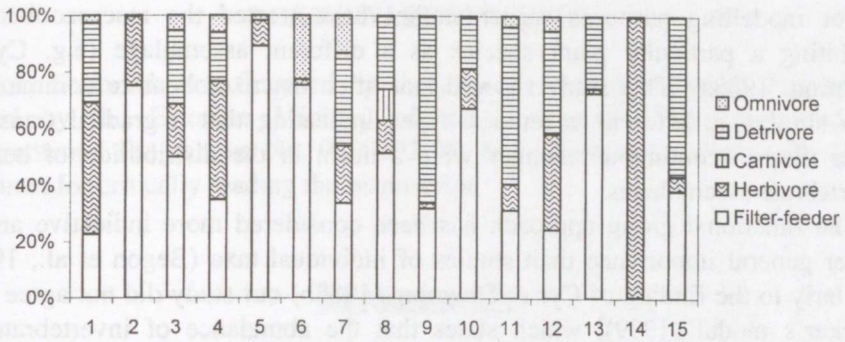


Fig. 8. The proportion of different feeding groups at studied phyto-benthic assemblages. For the code see Table 1.

DISCUSSION

The present study is a first attempt at quantitative estimation of the effect of various environmental variables on the structure of invertebrate assemblages in the phytal zone of the north-eastern Baltic Sea. Previously multivariate approaches have been successfully used to predict the structure of phyto-benthic assemblages in the Baltic Sea (Kautsky & van der Maarel, 1990; Kautsky, H., 1995). In these studies, however, the factors that determine the differences between animal assemblages remained less clear.

This study demonstrated that phyto-benthos was a key factor structuring the macrozoobenthic assemblages in Estonian coastal waters. According to our results, the abundance and biomass values of benthic invertebrates were lower in unvegetated areas as compared to vegetated areas. Earlier studies have led to controversial results when comparing benthic fauna between vegetated and unvegetated areas. Different authors have shown that species number and richness were either greater in areas with algae (Nicholls et al., 1981; Cyr & Downing, 1988a) or in unvegetated areas (Breber, 1985) or similar in vegetated and unvegetated areas (Soulsby et al., 1982). Berg et al. (1997) showed that plant biomass rather than vegetation type appears to determine the characteristics of the macroinvertebrate community.

Based on our data benthic invertebrates were highly selective about phyto-benthic assemblages and the differences in preference depended on the invertebrate species considered. However, some habitats (e.g. *Chara*, *Pilayella*, and *Furcellaria*) were preferred over others. *Pilayella* was previously shown to support a high biomass of herbivores (Kangas et al., 1982) and *Furcellaria* a high biomass of *Mytilus* (Kautsky, N., 1974). Higher biomass in *Chara* may be due to detrital enrichment reflected by the high proportion of detrivores in the area.

For modelling purposes earlier studies have treated the macrozoobenthos inhabiting a particular plant species as a different assemblage (e.g. Cyr & Downing, 1988a). This study showed that often macrozoobenthic communities were similar at different vegetation types indicating that a gradual transition rather than discontinuous changes were a norm in the distribution of benthic invertebrate assemblages.

The functional group approach has been considered more indicative and of higher general importance than studies of individual taxa (Begon et al., 1996). Similarly to the finding of Cyr & Downing (1988b) our study did not agree with Kreeker's model (1939), which states that the abundance of invertebrates is higher on plants with finely dissected leaves. Generally, we observed higher abundances and biomasses of invertebrates in perennial plants and algae with strong thalli than in annual and filamentous algae. The negative effect of filamentous algae on macrozoobenthos may be due to the decomposition of large amounts of algae, which may result in temporary anoxic conditions (Norkko & Bonsdorff, 1996). In many cases, however, filamentous algae do not form a barrier between infauna and the water column and, hence, they provide infauna a refuge from physical stress or predation pressure. Similarly to Hull (1987) we found higher numbers of *Macoma balthica* in the case of a greater filamentous algal cover.

Higher preference for the algae with strong thalli may be attributed to the higher average invertebrate biomass in *Furcellaria* assemblages. In the deeper areas where the sediments are finer, the structure of macrozoobenthos is mainly determined by nutrient input and properties of substrate – either primary substrate or the type of algal canopy. The loose-lying *Furcellaria* contributes significantly to the increase in the biomass of macrozoobenthos in the deeper parts of the Väinameri Sea by offering an appropriate substrate for *Mytilus edulis*. Besides, the thick mat of *Furcellaria* is expected to protect soft-sediment invertebrates effectively from fish predation.

To conclude, we can say that biotic factors (e.g. phytobenthic species) were superior over abiotic factors in describing the structure of macrozoobenthic assemblages in the phytal zone. Macrozoobenthos in different phytobenthos species were not necessarily different, indicating that different algal species had similar functions for benthic invertebrates. Macrozoobenthos in *Fucus vesiculosus*, *Furcellaria lumbricalis*, and *Pilayella littoralis*–*Polysiphonia nigrescens*–*Furcellaria lumbricalis* dominated assemblages differed significantly from other phytobenthic assemblages. *Chara* spp., *Pilayella littoralis*, and *Furcellaria lumbricalis* dominated assemblages were preferred over other habitats and species with strong thalli over filamentous algae. Many benthic invertebrates use *Zannichellia*, *Chara*, and *Fucus* mainly as feeding grounds (high proportion of herbivores) whereas for *Furcellaria*, *Chorda*, and *Sphacelaria* they serve as secondary substrate (high proportion of filter feeders).

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PÕHJAELOUVIISILISTE SELGROOTUTE LEVIKUT LÄÄNEMERE KIRDEOSA TAIMESTIKUVÖÖNDIS MÕJUTAVAD FAKTORID

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Põhjaloostikku on uuritud Läänemere kirdeosa rannikumeres. Kasutades permutatsioonianalüüsi võrreldi põhjaloostiku kooslusi 14 taimekoosluses ning leiti faktorid, mis enim mõjutavad loomakoosluste struktuuri. Erinevaid

taimeliike asustavad põhjaloomastiku kooslused lähevad üksteiseks sujuvalt üle. Põhjaloomastik taimekooslustes, kus domineerisid *Fucus vesiculosus*, *Furcellaria lumbricalis*, *Pilayella littoralis* ja *Polysiphonia nigrescens*, erines statistiliselt enamikust uuritud kooslustest. Põhjaloomastiku koosluste struktuur taimestiku-võõndis oli rohkem määratud biotiliste faktorite poolt võrreldes abiotiliste faktoritega. Põhjaloomastik eelistas *Chara* spp., *Pilayella littoralis*'e ja *Furcellaria lumbricalis*'e domineerimisega kooslusi ning tugeva tallusega liike.

