

Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea)

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Received 2 June 2000, accepted 26 September 2000

Kotta, J. & Orav, H. 2001: Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). — *Ann. Zool. Fennici* 38: 163–171.

The relationships between the abundance and biomass structure of invertebrate assemblages and environmental variables were sought by using multivariate statistics. Sediment type explained the biggest part of the variation in invertebrate assemblages in the deeper areas and dominant macroalgae 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 poor when 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*.

Introduction

The exceptionally low species diversity as well as between-habitat diversity are the characteristics of the benthic assemblages of the Baltic Sea. Owing to salinity constraints, short developing time and isolation only a few species have adapted to live here (Segerstråle 1957, Hällfors *et al.* 1981). High levels of urbanisation and industrialisation may further reduce biodiversity (Ceder-

wall & Elmgren 1990, Bonsdorff *et al.* 1997a, 1997b, Gray 1997) as well as the functioning efficiency and resistance of the system (Naeem *et al.* 1994). As a result of the extensive supply of nutrients, the large macroalgal “blooms” and the mass drift of algae are increasingly observed in coastal ecosystems (Bonsdorff 1992, Morand & Briand 1996). In some areas the role of the algal mats are considered as a key factor in altering the normal functioning of benthic communities (Nork-

ko & Bonsdorff 1996a, 1996b). 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, Olenin & Leppäkoski 1999). Similarly to eutrophication, biological invasions may severely affect diversity in the area (Leppäkoski 1991, Mills *et al.* 1993, Carlton 1996, Gollasch & Leppäkoski 1999).

The Väinameri contains a large number of different habitats and has a singularly high benthic diversity compared to other regions in the north-eastern Baltic Sea (Järvekülg 1970). The entire area is shallow, emphasizing the importance of benthic macroalgae in the dynamics of macrozoobentos. An extensive part of the Väinameri is covered by a unique assemblage of a loose-lying macroalgae *Furcellaria lumbricalis* (Trei 1970). In some respect this community resembles the algal mats described above, though the alga is coarser in its structure. However, *F. lumbricalis* offers a mat forming “nuisance” algae such as *Pilayella littoralis* the secondary substrate, which facilitates its development in large quantities. In spite of the fact that the invertebrate and macro-algal assemblages are relatively well described (Järvekülg 1970, Trei 1970) there is no information as to how benthic macroalgae contribute to the faunal diversity in the area.

The aim of this study is to provide the relevant information for the conservation and management of benthic assemblages. We examined the role of macroalgae in the variability of macrozoobenthos in the Väinameri region. Besides biotic variables the relationships between sediment type, depth 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. The named negative effects have been previously attributed to accumulating filamentous algae e.g. *P. littoralis* and *Cladophora glomerata* (Bonsdorff 1992, Norkko & Bonsdorff 1996a, 1996b).

Study area

The Väinameri (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) in comparison with 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 from 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).

Material and methods

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. The risk of missing extreme seasonal events in the phyto- and zoobenthos assemblages is low. However, as phytobenthic assemblages are best developed in August (TeinaNord 1996), the mapping was done during that time of the year. Samples were collected with a Tvärminne sampler (catching surface 315 cm²; Kangas 1972) on silty, sand or gravel bottoms and with a suction sampler (catching surface 315 cm²; Hiscock & Hoare 1973) on boulders and limestone. Samples below 0.5 m were

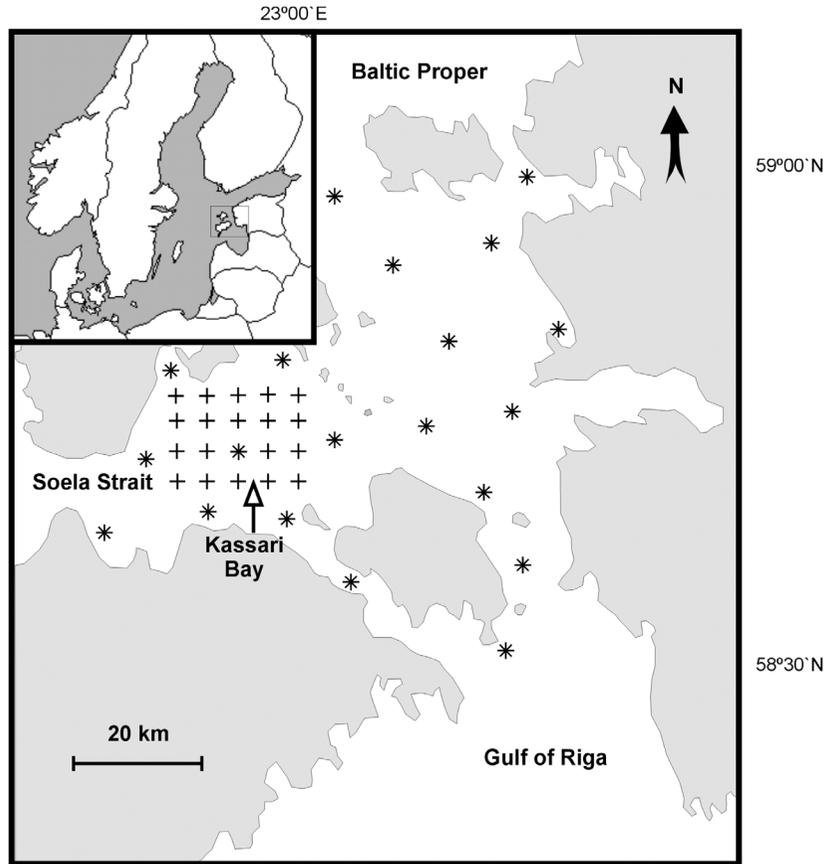


Fig. 1. Study area. The stars represent the grid of sampling stations in the whole Väinameri area and the crosses that of Kassari Bay, respectively.

taken by SCUBA diving. Three random samples were taken from each site. In order to better distinct infauna and the species associated with free-floating algae in the Kassari Bay the samples were split before sieving into two parts. The layer of *F. lumbricalis* was gently separated from the remaining sample by cutting the sample at the water-sediment interface with a small plastic spade. Care was taken not to resuspend the 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.

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

shells.

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. An 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). A BIO-ENV test was used to demonstrate the importance of different environmental variables in determining the structure of macrobenthic assemblages in the area.

Results

According to non-metric multidimensional scaling (MDS), benthic invertebrate assemblages did not form clearly distinguished groups in terms of abundance and biomass structure. 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.

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

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
Sediment	0.105	0.084
Depth	0.118	0.112
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

($p = 0.05$).

The aforementioned differences were mainly due to the dominance structure of bivalves and gastropods. *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* prevailed on all studied sediment types. Besides, stone bottoms were characterised by a higher density of *Gammarus* spp. (Tables 2 and 3).

F. lumbricalis was the most prevalent phyto-benthos species in the Väinameri followed by *P. littoralis* and *Fucus vesiculosus*. 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 and *Hydrobia* spp. and a lower biomass of *M. balthica*. *F. lumbricalis* community had a higher abundance and biomass of *M. edulis*. For other differences see Tables 4 and 5.

When only *F. lumbricalis* assemblage was concerned (Kassari Bay), the 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 and 0.065, respectively) structure in the 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. 2A and Table 6).

M. balthica was the most prevalent species in the sediment. *Cerastoderma glaucum*, *M. arenaria* and *Marenzelleria viridis* 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. 2B). As an exception, the biomass of *M. viridis* increased with the coverage of *F. lumbricalis* (Fig. 2C).

Table 2. Mean abundance values (ind. m⁻²) of dominant macrozoobenthic taxa at different sediment types in the Väinämeri. The code of sediment is as follows: 1 — stone, 2 — pebbly sand, 3 — gravel, 4 — coarse sand, 5 — medium sand, 6 — fine sand, 7 — silty sand, 8 — clayey sand, 9 — sandy clay, 10 — silt, 11 — clay.

Taxa	1	2	3	4	5	6	7	8	9	10	11
Total abundance	12 238	4 487	7 018	1 578	2 714	17 226	5 354	1 392	5 513	24 816	7 980
<i>Bathyporeia pilosa</i>	0	0	0	0	0	0	528	0	0	0	0
Chironomidae l.	323	0	203	0	213	0	23	0	14	829	0
<i>Cerastoderma glaucum</i>	66	0	493	0	213	0	886	696	44	33	116
<i>Corophium volutator</i>	447	77	58	70	8	1 102	95	348	138	414	30
<i>Gammarus</i> juv.	2 038	0	0	0	15	0	23	0	77	0	0
<i>Hydrobia</i> spp.	2 270	2 088	2 088	603	1 291	12 528	2 675	0	441	7 855	107
<i>Jaera albifrons</i>	630	58	87	0	0	0	0	0	148	2 295	0
<i>Lymnaea peregea</i>	166	0	58	0	23	0	0	0	0	1 094	29
<i>Mya arenaria</i>	149	39	116	70	104	406	199	116	394	1 375	79
<i>Macoma balthica</i>	141	446	1 740	545	228	2 552	498	116	1 200	522	692
<i>Mytilus edulis</i>	1 574	251	319	151	286	0	144	0	1 618	6 678	176
<i>Nereis diversicolor</i>	83	77	290	35	89	406	0	116	433	472	482
<i>Oligochaeta</i>	83	232	1 160	23	77	0	0	0	514	17	6 103
<i>Monoporeia affinis</i>	0	831	0	0	43	0	0	0	92	108	0
<i>Theodoxus fluviatilis</i>	945	116	290	81	62	0	93	0	1	224	0

Table 3. Mean biomass values (g m⁻²) of dominant macrozoobenthic taxa at different sediment types in the Väinämeri. For the code of sediment see Table 2.

Taxa	1	2	3	4	5	6	7	8	9	10	11
Total biomass	58.9	19.5	34.5	43.1	26.0	85.8	78.9	72.2	159.9	149.0	41.5
<i>Bithynia tentaculata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Chironomidae l.	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cerastoderma glaucum</i>	0.5	0.0	4.4	0.0	4.6	0.0	2.8	56.6	6.8	0.6	5.3
<i>Corophium volutator</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
<i>Gammarus</i> juv.	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus oceanicus</i>	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gammarus zaddachi</i>	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hydrobia</i> spp.	2.2	1.2	0.9	0.4	1.6	10.8	2.2	0.0	0.2	8.4	0.1
<i>Lymnaea peregea</i>	0.4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.1
<i>Mya arenaria</i>	3.4	7.1	2.8	19.5	8.7	18.2	49.2	1.0	33.2	11.3	10.5
<i>Macoma balthica</i>	5.5	8.5	23.0	18.7	7.2	45.1	23.2	13.7	56.6	18.9	21.2
<i>Mytilus edulis</i>	25.6	2.0	0.8	3.1	2.7	0.0	0.7	0.0	61.2	106.6	3.4
<i>Marenzelleria viridis</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1
<i>Nereis diversicolor</i>	0.0	0.0	0.1	0.5	0.2	0.1	0.0	0.7	1.7	0.3	0.8
<i>Oligochaeta</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
<i>Saduria entomon</i>	0.0	0.0	0.4	0.0	0.3	11.6	0.0	0.0	0.0	0.0	0.0
<i>Theodoxus fluviatilis</i>	17.8	0.5	2.1	0.9	0.6	0.0	0.6	0.0	0.0	0.0	0.0

Discussion

No single environmental variable structuring the macrozoobenthos of the Väinameri was found, indicating both hydrodynamic instability and diversity of the system. 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). 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). Hence, it may explain the higher importance of macrophytes there.

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. The fluffy layer of sediment was substantially thicker under *F. lumbricalis* as compared to unvegetated areas indicating that the algae may induce higher sediment stability. Besides, it is likely that the compactness of *F. lumbricalis* offers infauna a protection from fish predation. However, our results demonstrated that the infaunal density did not

Table 4. Mean abundance values (ind. m⁻²) of dominant macrozoobenthic taxa at prevalent vegetation types and unvegetated areas in the Väinameri.

Taxa	<i>Cladophora</i>	<i>Fucus</i>	<i>Furcellaria</i>	<i>Pilayella</i>	Unvegetated
Total abundance	2 204	2 958	4 176	25 520	5 127
<i>Chironomidae</i> l.	0	0	0	1 856	247
<i>Cerastoderma glaucum</i>	348	0	0	0	321
<i>Corophium volutator</i>	0	77	0	0	174
<i>Gammarus</i> juv.	0	232		9 628	39
<i>Hydrobia</i> spp.	0	1 547	0	0	2 018
<i>Idotea chelipes</i>	0	39	0	232	15
<i>Jaera albifrons</i>	348	39	0	1 972	39
<i>Lymnaea peregra</i>	0	0	0	0	305
<i>Macoma balthica</i>	116	77	271	0	563
<i>Mytilus edulis</i>	116	116	3 789	1 160	529
Oligochaeta	0	174	0	0	118
<i>Theodoxus fluviatilis</i>	0	116	77	232	155
<i>Prostoma obscurum</i>	1 160	155	0	116	2

Table 5. Mean biomass values (g m⁻²) of dominant macrozoobenthic taxa at prevalent vegetation types and unvegetated areas in the Väinameri.

Taxa	<i>Cladophora</i>	<i>Fucus</i>	<i>Furcellaria</i>	<i>Pilayella</i>	Unvegetated
Total biomass	1.7	15.3	63.1	15.6	66.2
<i>Cerastoderma glaucum</i>	0.1	0.0	0.0	0.0	4.3
<i>Gammarus</i> juv.	0.0	0.2	0.0	1.5	0.0
<i>Hydrobia</i> spp.	0.0	1.0	0.0	0.0	1.8
<i>Mya arenaria</i>	0.0	5.4	0.0	0.0	10.3
<i>Macoma balthica</i>	0.5	5.8	24.7	0.0	23.7
<i>Mytilus edulis</i>	0.5	1.8	37.0	10.7	22.4
<i>Saduria entomon</i>	0.0	0.0	0.7	0.0	0.6
<i>Theodoxus fluviatilis</i>	0.0	0.5	0.7	0.7	1.5

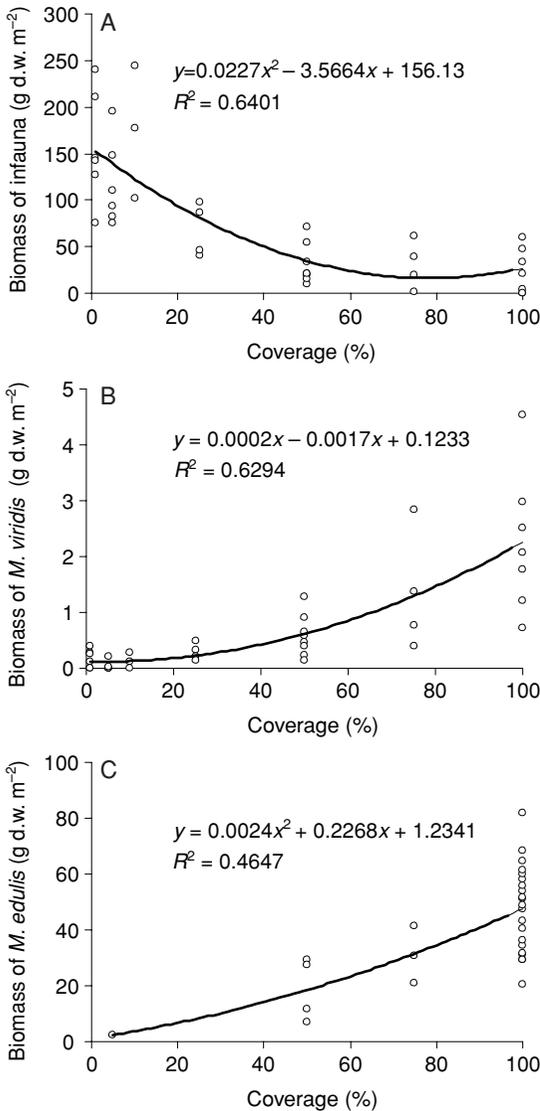


Fig. 2. The relationship between the coverage of *Furcellaria lumbricalis* and the biomass of *Mytilus edulis* (A), infauna (B) and *Marenzelleria viridis* (C) in Kassari Bay in 1995.

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 ben-

thic invertebrates under *F. lumbricalis* may be due to the decomposition of epiphytic filamentous algae attached to *F. lumbricalis* resulting in calmer weather 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. Unfortunately we do not have substantial information to qualify this further. However, comparable negative effect of drifting filamentous algal mats on benthic invertebrates has been previously documented elsewhere in the Baltic Sea (e.g. Norkko & Bonsdorff 1996a, 1996b). These studies demonstrated that in most severe cases the algal mats may wipe off all infauna and significantly reduce benthic inverte-

Table 6. Mean abundance (ind. m⁻²) and biomass values (g m⁻²) of dominant macrozoobenthic taxa in Kassari Bay. The code is as follows: 1 — macrozoobenthos in sediment, *F. lumbricalis* present, 2 — macrozoobenthos in the layer of *F. lumbricalis*, 3 — macrozoobenthos in sediment, no *F. lumbricalis*.

Taxa	1	2	3
Total abundance	989	4 176	2 385
<i>Asellus aquaticus</i>	0	0	12
<i>Cerastoderma glaucum</i>	183	0	311
<i>Corophium volutator</i>	21	0	130
<i>Gammarus</i> juv.	22	0	64
<i>Halicryptus spinulosus</i>	0	0	6
<i>Hydrobia</i> spp.	0	0	24
<i>Jaera albifrons</i>	0	0	12
<i>Mya arenaria</i>	126	0	222
<i>Macoma balthica</i>	370	271	548
<i>Mytilus edulis</i>	148	3 789	894
<i>Marenzelleria viridis</i>	79	0	0
<i>Nereis diversicolor</i>	27	0	52
<i>Saduria entomon</i>	3	39	0
<i>Theodoxus fluviatilis</i>	9	77	41
<i>Prostoma obscurum</i>	0	0	12
Total biomass	78.2	63.1	118.1
<i>Cerastoderma glaucum</i>	10.5	0.0	13.4
<i>Halicryptus spinulosus</i>	0.0	0.0	0.1
<i>Mya arenaria</i>	41.5	0.0	45.3
<i>Macoma balthica</i>	28.1	24.7	30.2
<i>Mytilus edulis</i>	2.3	37.0	28.4
<i>Marenzelleria viridis</i>	0.8	0.0	0.0
<i>Nereis diversicolor</i>	0.1	0.0	0.2
<i>Saduria entomon</i>	0.1	0.7	0.0
<i>Theodoxus fluviatilis</i>	0.1	0.7	0.3

brates 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, owing to the high hydrodynamic activity 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* assemblage in the deeper areas. Possible 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

This study was carried out within the framework of Estonian Governmental Programme no. 0200792s98 and Phytobenthos Monitoring Programme financed by the Estonian Ministry of the Environment.

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