

Phytobenthic microcoenoses along Estonian exposed seashores

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Abstract. Distribution and environmental range of phytobenthic microcoenoses along the exposed shores of the northeastern part of the Baltic Sea in Estonia are described. A total of 104 biomass samples were clustered into distinct micro-associations, and 35 composite samples into six community types. The *Fucus vesiculosus* community type is the most heterotoneous in the study area, including microcoenoses of various micro-associations. The other community types are more homotoneous. Phytobenthic microcoenoses at sites are related mainly to the depth of the seabed. Most of the microcoenoses have a more or less local distribution; only microcoenoses of the *Fucus vesiculosus* micro-association were found throughout the study area.

Key words: Baltic Sea, biomass, communities, distribution, micro-associations.

INTRODUCTION

The history of benthic macroalgal investigations along the Estonian shoreline dates back to the late 18th century. More than 150 published papers and manuscripts describe the species composition and the ecology of benthic macroalgae in the coastal areas of the southern part of the Gulf of Finland, northern part of the Gulf of Riga, and the West Estonian Archipelago area (Fischer, 1778; Gobi, 1874, 1877; Svedelius, 1902; Häyrén, 1929–30; etc.). Most of these publications have a strong floristic orientation. The first attempts to create a classification system for the benthic algal communities of Estonian coastal waters were made in the 1970s by Trei (1973) and Kukk (1978, 1979). These studies, quite similar in structure and principles of classification, are based on empirical interpretation of large amounts of qualitative and semi-quantitative data collected over several

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decades. Martin et al. (2000) developed a classification for benthic littoral communities of the West Estonian Archipelago area based on cluster analysis.

All the classification systems of phytobenthic vegetation elaborated in Estonia so far have been compiled on a community scale. Either the descriptive data generalized over the whole visually bordered community are used, or, in the case of quantitative studies, the data of small quadrats from one community are averaged and these composite samples (Gauch, 1982) are then subjected to clustering. The constitutional components (synusiae, microcoenoses) of phytobenthic communities have not been considered in Estonia or in the neighbouring Baltic countries. At the same time, these components represent a challenging problem in the detailed study of vegetation classification structure on different scales. The classification system obtained by composite samples lacks an overview of the infrastructure of communities. The high values of standard error, or coefficient of variation, calculated for cluster centroids cannot give more than a hint of the possible intricate community pattern. The use of two parallel classifications – one based on clustering of single small quadrats, and the other operating with composite samples – is a straightforward technique for identifying spatial homogeneity of communities (resp. vegetation belts), as well as internal homogeneity (*sensu* Nordhagen, 1943; Dahl, 1957) of community types.

In the last decades the methods of identifying the environmental factors and biotic interactions determining the structure and distribution of communities have developed rapidly. It has been found that in the Baltic Sea the formation of phytobenthic communities in the shallowest parts depends mostly on wave action, and in deeper areas, on the availability of light and suitable substrate, while biotic interactions have a minor role to play (Kautsky, 1988; Kautsky & van der Maarel, 1990; Kiirikki, 1996). In Estonian waters, phytobenthos–environment interactions have recently most thoroughly been studied in the Gulf of Riga and the Väinameri (Martin, 1999; Kautsky et al., 1999; Martin et al., 2000). The most important environmental factor determining the structure of phytobenthos in these areas is the nature of the substrate (Kautsky et al., 1999; Martin et al., 2000). The quantitative and qualitative characteristics of phytobenthos have a strong regional pattern in the Gulf of Riga (Martin, 1999) as well as in the Väinameri (Martin et al., 2000).

Comparison of community classifications from different periods reveals temporal alterations in species composition and abundance in communities. There can be small-scale local fluctuations of these parameters and large-scale irreversible changes over larger areas. Alterations in phytobenthic communities, e.g. the large-scale decline of *Fucus vesiculosus* during the last decades, have been described in many parts of the Baltic Sea (Kangas et al., 1982; Mäkinen et al., 1984; Vogt & Schramm, 1991; Rönnerberg et al., 1995; Schramm & Nienhuis, 1996). In Estonia, small-scale changes in phytobenthos composition have also been recorded (Kukk & Martin, 1992; Kotta et al., 2000).

The aim of the present study is (i) to establish and compare the classification systems of the phytobenthic vegetation of Estonian exposed coasts on a microcoenosis scale as well as on a community scale; (ii) to evaluate the correspondence

between the obtained results and community types of former investigations, and (iii) to estimate the environmental factors determining the distribution of micro-coenoses of different microassociations.

MATERIAL AND METHODS

Study area

The study area covers the northeast Baltic Sea including the northern and western coasts of Estonia (Fig. 1). Altogether, ten sites along the coast were investigated: Kunda, Eru, Lohusalu, and Nõva in the Gulf of Finland; Kõiguste in the Gulf of Riga; and Kaugatuma, Küdema, Kõpu, Saxby, and Tjuka in the Baltic Proper. The shoreline of the area is quite complex with many islands, islets, and bays. Study sites were chosen to represent the coastline free from direct riverine inputs and with similar exposure and bottom characteristics. The dominating substrates were limestone rock, stone, and sand; in most cases they formed an intermixed pattern. In Kõiguste, Kaugatuma, Saxby, Tjuka, Kõpu, Nõva, Lohusalu, and Kunda the substrate was a mixture of sand, gravel, and stones; in Küdema and Nõva there was limestone covered with granite stones. The salinity range along the studied coastline was from 7‰ on the Estonian western coast to 5‰ in the middle of the Gulf of Finland (Kukk, 1979; Trei, 1991).

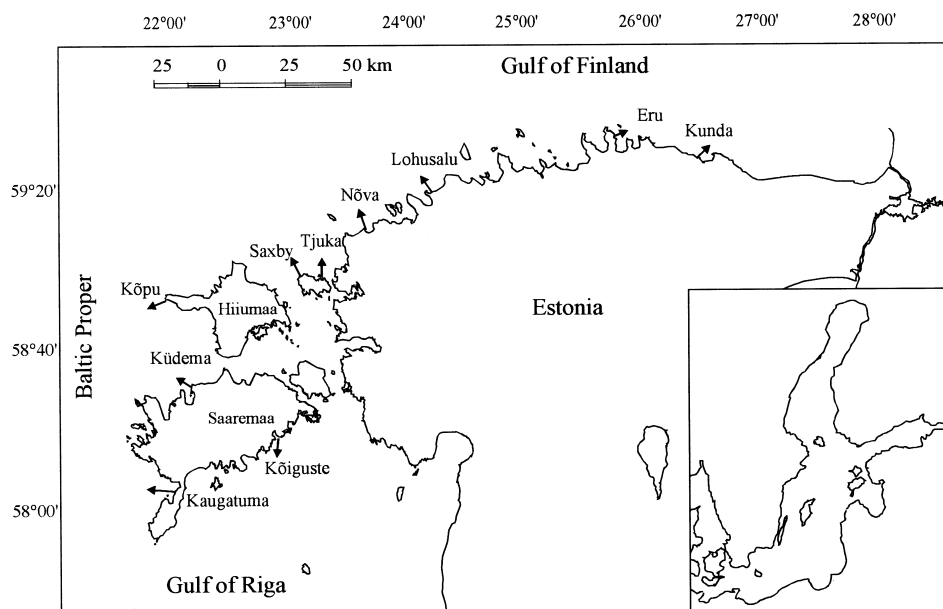


Fig. 1. Study area in the Baltic Sea and the location of sampling sites on the Estonian coast. Arrows mark the location and direction of transects.

Sampling

The sampling was performed from the end of July to the beginning of October 1998. A transect from the water's edge to the lower vegetation limit was used at each site in order to describe the bottom vegetation and collect samples. The transects were described and the samples were taken using SCUBA-diving techniques. The transects were of different lengths (0.2–6 km) depending on the slope of the shore. If the transect was short, the diver swam the whole distance; in long transects the divers performed 50–100 m subtransects at given depth intervals. Along each transect, the divers recorded the type of substrate and the exact depth according to depth gauge. In every vegetation belt, estimated according to the dominating plant species, quantitative samples were collected by tossing three frames at random. Square frames of 0.2×0.2 m were used. Whenever the composition of the dominating species changed or their total cover dropped to less than 25%, the belt was sampled again. The total number of samples collected and analysed during the present investigation was 104.

In the samples all specimens were identified, most of them to species level. *Chara* spp. and *Enteromorpha* spp. were identified to genus level, and the brown filamentous algae *Pilayella littoralis* and *Ectocarpus confervoides* were not separated. The nomenclature of algae is given according to Nielsen et al. (1995), and that of higher plants according to Leht (1999). The dry weight of the specimens of every taxon was measured; the samples were dried at 60°C for two weeks before weighing. The value of taxon biomass in the sample was calculated as dry weight per square metre.

Data processing

To evaluate the importance of exposure for bottom communities, the surface exposure index was calculated for each site according to Baardseth (1970). Substrate hardness was estimated by ordering the substrates from 1 (hard rock) to 11 (mud).

In order to select an optimal clustering method, various similarity measures (Manhattan distance, Euclidean distance, chord distance) and algorithms (single linkage, average linkage, minimal incremental sum of squares) were compared. The latter grouping algorithm and Euclidean distance gave the best interpretable results. Cluster analysis was performed in two stages. At first, data of single 0.2×0.2 m sample quadrats were used; after that, the data of three quadrats representing the same vegetation belt (community) were averaged, and these composite samples were treated as separate data sets. To reduce the influence of dominant taxa and to approximate the distribution of the species' values to a normal distribution, the data were log₁₀-transformed before clustering. Cluster analysis was carried out by means of the SYN-TAX 5.02 program package (Podani, 1993). The quality of the dendrogram was evaluated by the cophenetic correlation coefficient (Sokal & Rolf, 1973; Podani, 1994).

In order to measure the degree of mutual distinctness or continuity between clusters, the α -criterion (Duda & Hart, 1976) was used. To obtain a better interpretation of the estimates, the corresponding probabilities were applied as coefficients of indistinctness (CI) (Paal, 1987) instead of the direct values of the α -criterion. At first, all the dendrogram branches including at least three objects were considered as clusters. If the CI for the neighbouring clusters in the dendrogram was higher than 5.0, the clusters could be merged from a statistical point of view and the continuum analysis was started iteratively again. When merging the clusters their interpretability was also taken into account.

The difference between environmental conditions in clusters was tested by one-way analysis of variance, carried out by the program package STATISTICA 5.1 (StatSoft, Inc., 1998).

Ordination was performed by the program package CANOCO for Windows Version 4.02 (Ter Braak & Šmilauer, 1998); canonical correspondence analysis (CCA) with default settings was used. The significance of the first two ordination axes was tested by the Monte Carlo permutation test (199 unrestricted permutations). The importance of environmental variables was tested in forward-selection procedure using Monte Carlo permutation tests. The results of ordination analyses were visualized by means of the program package CanoDraw 3.0 (Šmilauer, 1992).

RESULTS AND DISCUSSION

Cluster analysis

The dendrogram of single quadrats has three large branches, all divided further into several smaller units (Fig. 2). On the basis of continuum analysis, a ten-cluster solution was accepted. The cophenetic correlation of the dendrogram is quite high (0.71), confirming a rather good correspondence between the dendrogram and the real data structure and the suitability of the chosen clustering algorithm. Taking into account that, in the current study, plants of all growth-forms occurring in the quadrats were considered, the term 'microcoenosis' is correct for these vegetation samples, while units of their classification can be called micro-associations (Barkman, 1964; Korchagin, 1976).

The first clearly separated branch of the dendrogram is divided into three clusters, all mutually indistinct ($CI_{1,2} = 43.4$, $CI_{1,3} = 33.4$, $CI_{2,3} = 73.1$). On that basis these clusters should be merged, but as they all have certain biological peculiarities the clusters were accepted despite their indistinctness. The first cluster includes epiphyte-rich (mainly filamentous brown algae) *Fucus vesiculosus* microcoenoses (Table 1); in the second cluster *F. vesiculosus* is a single dominant, and in the third cluster there are several comparatively abundant species (*Furcellaria lumbricalis*, *Polysiphonia fucoides*, *Elachista fucicola*, *Cladophora rupestris*) in addition to *F. vesiculosus* and filamentous brown algae. According of this, the first three clusters can be interpreted as variants of the *F. vesiculosus* dominated micro-association with a very high biomass. Clusters with dominating *F. vesiculosus* are all clearly distinct from the others.

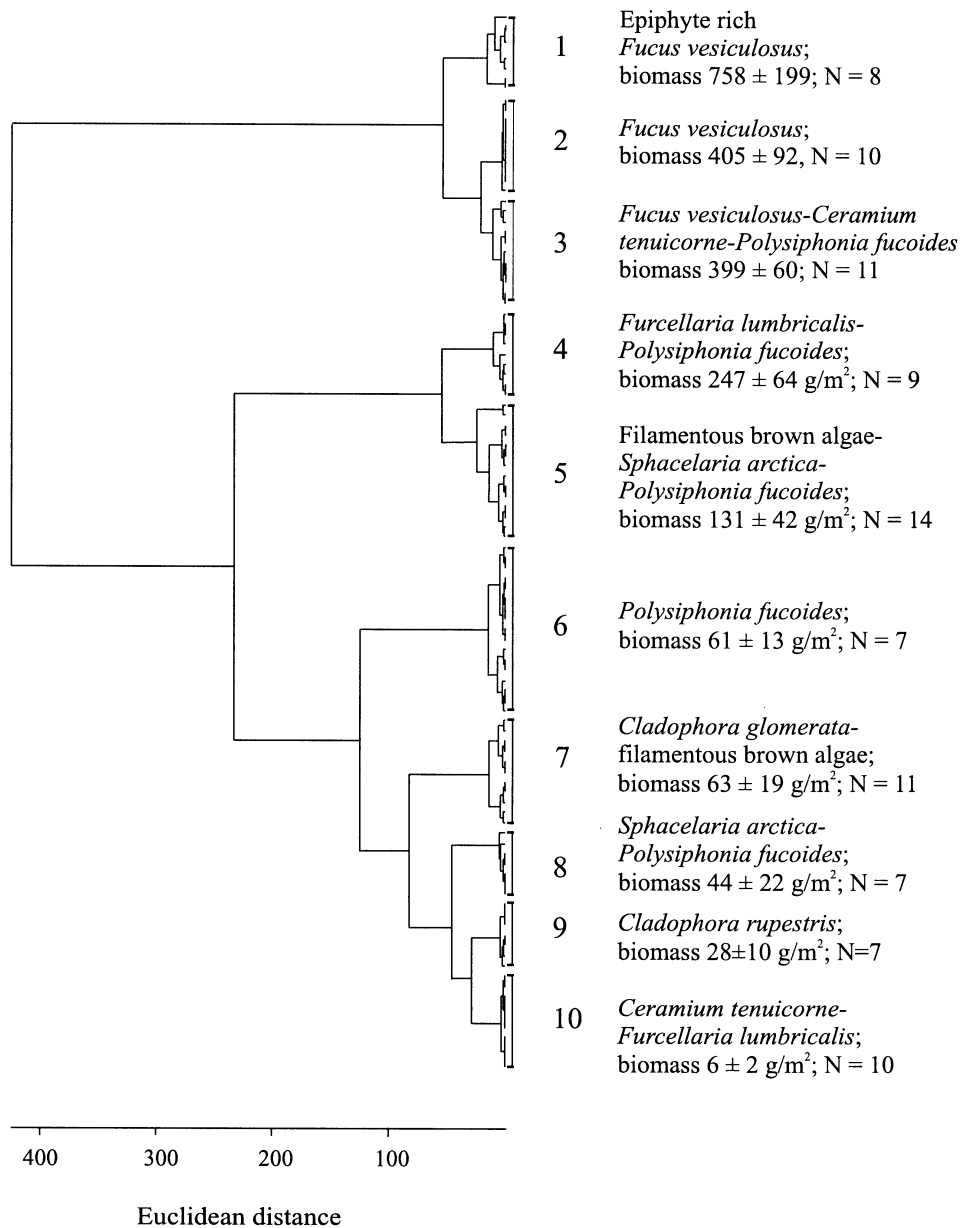


Fig. 2. Classification dendrogram of the phytobenthic microcoenoses. The dominant species, mean biomass value \pm standard error of the mean, and the number of samples in the cluster (N) are shown by the number of the cluster.

Table 1. Centroids of micro-associations (species mean biomass \pm error of the mean). Only species with an average dry biomass over 0.1 g/m² in at least one cluster are presented

Species	Cluster										
	1	2	3	4	5	6	7	8	9	10	
<i>Potamogeton pectinatus</i>	-	-	-	-	10.6 \pm 9.1	-	-	-	-	-	0.0 \pm 0.0
<i>Schoenoplectus tabernaemontanii</i>	-	-	-	-	-	-	-	-	-	-	0.8 \pm 0.7
<i>Zannichellia palustris</i>	7.3 \pm 7.3	-	-	0.1 \pm 0.0	0.0 \pm 0.0	-	0.2 \pm 0.1	-	0.2 \pm 0.2	4.7 \pm 4.6	
<i>Zostera marina</i>	-	-	0.0 \pm 0.0	0.2 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0	-	-	-	0.12 \pm 0.12	
<i>Chorda filum</i>	0.4 \pm 0.4	0.4 \pm 0.4	-	-	0.1 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0	-	-	-	
<i>Dictyosiphon foeniculaceus</i>	0.1 \pm 0.1	-	0.1 \pm 0.1	0.9 \pm 0.8	0.8 \pm 0.5	0.3 \pm 0.2	0.1 \pm 0.1	0.0 \pm 0.0	-	0.0 \pm 0.0	
<i>Elachista fucicola</i>	14.0 \pm 9.2	0.1 \pm 0.1	1.5 \pm 0.7	-	-	-	-	-	-	-	
<i>Fucus vesiculosus</i>	561.4 \pm 196.9	402.7 \pm 92.6	370.6 \pm 56.8	-	0.2 \pm 0.2	-	4.8 \pm 2.9	-	0.3 \pm 0.3	0.0 \pm 0.0	
Filamentous brown algae	165.1 \pm 19.7	0.1 \pm 0.1	16.4 \pm 4.8	10.7 \pm 2.9	82.2 \pm 20.1	5.6 \pm 2.2	11.3 \pm 4.1	0.1 \pm 0.1	0.0 \pm 0.0	0.7 \pm 0.2	
<i>Sphacelaria arctica</i>	0.1 \pm 0.1	0.0 \pm 0.0	1.5 \pm 1.3	4.8 \pm 2.0	12.4 \pm 3.2	0.1 \pm 0.3	0.6 \pm 0.3	33.2 \pm 12.9	-	0.1 \pm 0.0	
<i>Ceramium nodulosum</i>	-	-	-	4.3 \pm 4.0	-	0.1 \pm 0.1	0.4 \pm 0.3	0.3 \pm 0.3	0.02 \pm 0.02	-	
<i>Ceramium tenuicorne</i>	3.7 \pm 1.3	0.1 \pm 0.1	0.7 \pm 0.2	14.8 \pm 6.9	0.6 \pm 0.3	3.6 \pm 1.9	5.1 \pm 2.0	0.1 \pm 0.0	3.94 \pm 1.98	3.1 \pm 1.4	
<i>Furcellaria lumbricalis</i>	0.4 \pm 0.3	-	4.3 \pm 3.9	189.8 \pm 43.9	7.3 \pm 2.1	0.0 \pm 0.0	0.0 \pm 0.0	0.4 \pm 0.3	-	5.8 \pm 3.9	
<i>Coccolithus truncatus</i>	-	-	-	0.2 \pm 0.1	0.1 \pm 0.1	0.0 \pm 0.0	-	0.0 \pm 0.0	-	-	
<i>Polysiphonia fucoides</i>	4.7 \pm 2.4	-	2.5 \pm 1.3	19.7 \pm 2.4	15.0 \pm 5.1	49.0 \pm 6.8	1.4 \pm 0.9	7.4 \pm 6.5	-	0.1 \pm 0.1	
<i>Rhodomela confervoides</i>	-	-	0.1 \pm 0.1	0.6 \pm 0.3	1.2 \pm 0.8	0.8 \pm 0.8	-	2.2 \pm 2.1	-	-	
<i>Chara</i> spp.	0.2 \pm 0.2	-	-	-	0.0 \pm 0.0	-	-	-	-	1.8 \pm 1.0	
<i>Cladophora glomerata</i>	0.1 \pm 0.0	0.7 \pm 0.7	0.1 \pm 0.0	-	0.0 \pm 0.0	-	37.1 \pm 6.9	-	1.0 \pm 1.0	0.4 \pm 0.2	
<i>Cladophora rupestris</i>	0.0 \pm 0.0	0.8 \pm 0.5	1.1 \pm 1.1	0.5 \pm 0.3	0.7 \pm 0.5	0.3 \pm 0.2	1.9 \pm 1.5	0.0 \pm 0.0	21.4 \pm 6.0	0.2 \pm 0.1	
<i>Enteromorpha</i> spp.	-	0.0 \pm 0.0	0.2 \pm 0.2	-	-	-	0.1 \pm 0.1	-	0.7 \pm 0.6	0.9 \pm 0.7	

Micro-associations of *Furcellaria lumbricalis*–*Polysiphonia fucooides* (cluster 4) and filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucooides* (cluster 5) form the next rather clearly separated branch on the dendrogram. The remaining five clusters are mutually more related, but still reliably distinct. The 6th cluster can be called the *Polysiphonia fucooides* micro-association, followed by the *Cladophora glomerata*–filamentous brown algae micro-association, *Sphacelaria arctica*–*Polysiphonia fucooides* micro-association, *Cladophora rupestris* micro-association, and *Ceramium tenuicorne*–*Furcellaria lumbricalis* micro-association (Table 1).

The classification of composite samples resulted in six almost distinct clusters; the cophenetic correlation coefficient of the dendrogram (Fig. 3) is 0.61. Only the

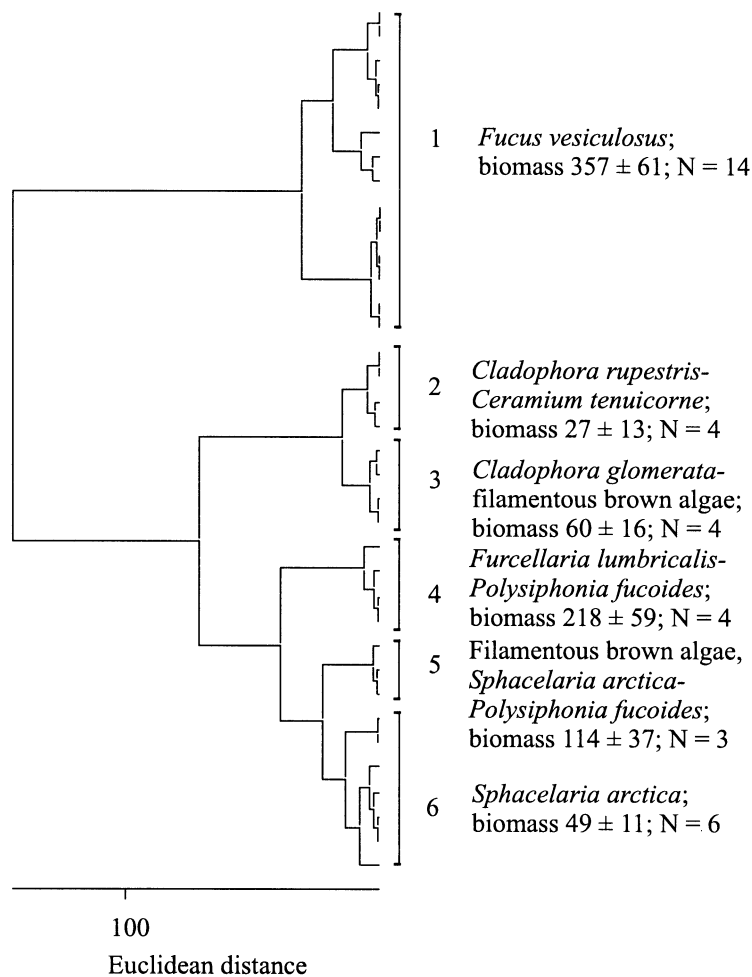


Fig. 3. Classification dendrogram of the composite samples (communities). Notation as in Fig. 2.

2nd and 6th clusters are not well separated according to statistical testing ($CI_{2,6} = 10.9$); the observed indistinctness is caused by the low biomass of the species in both respective clusters in comparison with other clusters rather than by an overlapping species list.

In this classification structure the community type dominated by *F. vesiculosus* is again clearly distinct from the other types (Table 2). The *Cladophora rupestris*–*Ceramium tenuicorne* and *Cladophora glomerata*–filamentous brown algae community types constitute the next two quite closely related clusters. The *Furcellaria lumbricalis*–*Polysiphonia fucoides*, filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucoides*, and *Sphacelaria arctica* community types represent the third, and last, larger branch of the dendrogram. It should be stressed here that the three small sample quadrats used for compiling composite samples do not always reliably represent the vegetation on a community scale, therefore the obtained clusters can be interpreted with certain reservations as community types.

Table 2. Centroids of plant communities (species mean \pm error of the mean). Only species with an average dry biomass over 0.1 g/m² in at least one cluster are included

Species	Cluster					
	1	2	3	4	5	6
<i>Potamogeton pectinatus</i>	3.5 \pm 3.0	–	–	–	0.1 \pm 0.2	0.0 \pm 0.0
<i>Schoenoplectus tabernaemontanii</i>	–	–	–	–	–	0.5 \pm 0.5
<i>Zannichellia palustris</i>	1.4 \pm 1.4	5.9 \pm 5.9	0.2 \pm 0.1	0.1 \pm 0.0	0.0 \pm 0.1	0.0 \pm 0.1
<i>Zostera marina</i>	–	–	–	0.2 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1
<i>Chorda filum</i>	0.2 \pm 0.1	–	0.0 \pm 0.0	0.1 \pm 0.1	–	–
<i>Dictyosiphon foeniculaceus</i>	0.1 \pm 0.03	0.0 \pm 0.0	0.1 \pm 0.1	0.8 \pm 0.7	1.2 \pm 2.0	0.1 \pm 0.1
<i>Elachista fucicola</i>	3.1 \pm 2.7	–	–	–	–	–
<i>Fucus vesiculosus</i>	283.6 \pm 47.9	5.1 \pm 5.1	4.6 \pm 2.3	20.4 \pm 20.4	–	0.0 \pm 0.0
Filamentous brown algae	49.9 \pm 18.9	0.7 \pm 0.4	10.4 \pm 5.2	9.4 \pm 4.2	68.2 \pm 55.1	1.2 \pm 1.1
<i>Sphacelaria arctica</i>	0.4 \pm 0.2	–	0.5 \pm 0.5	4.8 \pm 2.5	18.5 \pm 9.4	11.7 \pm 7.0
<i>Ceramium nodulosum</i>	–	0.0 \pm 0.0	0.4 \pm 0.4	3.2 \pm 3.0	–	0.2 \pm 0.1
<i>Ceramium tenuicorne</i>	1.8 \pm 0.6	3.3 \pm 1.6	4.7 \pm 2.9	11.4 \pm 6.2	0.2 \pm 0.0	2.8 \pm 1.7
<i>Furcellaria lumbricalis</i>	2.0 \pm 1.2	–	0.0 \pm 0.0	142.6 \pm 35.9	7.3 \pm 5.3	4.2 \pm 2.6
<i>Coccotylus truncatus</i>	–	–	–	0.1 \pm 0.1	0.1 \pm 0.2	–
<i>Polysiphonia fucoides</i>	9.9 \pm 4.2	–	1.3 \pm 0.9	24.0 \pm 5.7	16.2 \pm 24.1	4.0 \pm 11.7
<i>Rhodomela confervoides</i>	–	–	–	0.5 \pm 0.3	1.8 \pm 2.9	1.7 \pm 1.1
<i>Chara</i> spp.	0.0 \pm 0.0	–	–	–	0.0 \pm 0.0	1.3 \pm 1.3
<i>Cladophora glomerata</i>	0.2 \pm 0.2	0.1 \pm 0.1	34.6 \pm 9.2	–	–	0.2 \pm 0.2
<i>Cladophora rupestris</i>	1.0 \pm 0.5	11.5 \pm 6.1	2.5 \pm 1.7	0.8 \pm 0.5	0.0 \pm 0.0	0.0 \pm 0.0
<i>Enteromorpha</i> spp.	0.1 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.4	–	–	0.6 \pm 0.6

Micro-associations and community types

Comparison of microcoenoses and communities shows that on both scales the most frequent classification units, dominated by *F. vesiculosus*, are conspicuously heterotoneous. On the microcoenosis scale, three variants of the respective micro-association were established; on the community scale, the corresponding branch of the dendrogram consists also of three sub-branches (Fig. 3). Since the input data for cluster analysis were different in both cases, we cannot find a one-to-one correspondence between the two considered clusters. However, if the position of single microcoenoses belonging to various clusters is traced, the micro-association variants are in general reflected also as community type variants. In addition, the composite samples that form the *Fucus vesiculosus* community type include several samples from the filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucoides*, *Polysiphonia fucoides*, and *Ceramium tenuicorne*–*Furcellaria lumbricalis* micro-associations (Table 3). Many authors (Wærn, 1952; Kangas et al., 1982; Kautsky, 1988; etc.) have also emphasized the spatial heterogeneity of the *F. vesiculosus* dominated communities.

In the communities of *Cladophora rupestris*–*Ceramium tenuicorne* type the microcoenoses of the *Cladophora rupestris* and *Ceramium tenuicorne*–*Furcellaria lumbricalis* micro-associations are almost equally represented (Table 3). The

Table 3. Correspondence between the phytobenthic micro-associations and community types

Micro-association	Community type*					
	1	2	3	4	5	6
1. Epiphyte rich <i>Fucus vesiculosus</i>	8	–	–	–	–	–
2. <i>Fucus vesiculosus</i>	10	–	–	–	–	–
3. <i>Fucus vesiculosus</i> and other species	10	1	–	–	–	–
4. <i>Furcellaria lumbricalis</i> – <i>Polysiphonia fucoides</i>	–	–	–	9	–	–
5. Filamentous brown algae– <i>Sphacelaria arctica</i> – <i>Polysiphonia fucoides</i>	5	–	–	–	9	–
6. <i>Polysiphonia fucoides</i>	5	–	–	2	–	10
7. <i>Cladophora glomerata</i> – filamentous brown algae	–	–	11	–	–	–
8. <i>Sphacelaria arctica</i> – <i>Polysiphonia fucoides</i>	–	–	–	–	–	7
9. <i>Cladophora rupestris</i>	–	6	1	–	–	–
10. <i>Ceramium tenuicorne</i> – <i>Furcellaria lumbricalis</i>	4	5	–	–	–	4

* The number of microcoenoses of different type (0.2 × 0.2 m samples) included in the respective community type. For names of community types see Fig. 3.

Cladophora glomerata–filamentous brown algae community type and the consubstantial micro-association are very similar to each other, the same can be followed by *Furcellaria lumbricalis*–*Polysiphonia fucooides* community type and micro-association. Other authors have not referred to the heterogeneity of these communities either. The communities of filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucooides* include only the samples from the respective microcoenoses. In the communities of *Sphacelaria arctica* type the microcoenoses of *Polysiphonia fucooides*, *Sphacelaria arctica*–*Polysiphonia fucooides*, and *Ceramium tenuicorne*–*Furcellaria lumbricalis* are represented. There is no corresponding community type for the *Polysiphonia fucooides* micro-association. Therefore, in the course of averaging and new clustering, the samples of these microcoenoses were distributed between the *Fucus vesiculosus*, *Furcellaria lumbricalis*–*Polysiphonia fucooides*, and *Sphacelaria arctica* community types.

Distribution of microcoenoses

The *Fucus vesiculosus* micro-associations are the most widely represented in the study area (Fig. 4). The microcoenoses dominated by *F. lumbricalis* and *P. fucooides* were found only near Vormsi Island. The microcoenoses of filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucooides* type occur in the coastal waters of Vormsi Island (Tjuka) and Saaremaa Island (Kaugatuma, Küdema). The *Polysiphonia fucooides* type microcoenoses were found from Küdema, Kõpu, Saxby, and Nõva; microcoenoses of *Cladophora glomerata*–filamentous brown algae type were found from Kaugatuma, Küdema, and Nõva. Microcoenoses of the *Sphacelaria arctica*–*Polysiphonia fucooides* micro-association were represented only at Kõiguste and Eru, while microcoenoses of *Cladophora rupestris* and *Ceramium tenuicorne*–*Furcellaria lumbricalis* type occurred only in sites along the coast of the Gulf of Finland.

The limited geographical distribution of certain types of microcoenoses can be explained by the salinity range of the species. No *Furcellaria lumbricalis*–*Polysiphonia fucooides* microcoenoses were found in the Gulf of Finland, probably because of salinity limitation. *Furcellaria lumbricalis* communities have previously been found only in waters with a salinity higher than 5.8‰ (Kukk, 1978; Trei, 1991). The distribution of samples with *P. fucooides* is concentrated in the western part of the study area. The salinity boundary of this species lies in the middle of the Gulf of Finland (Kukk, 1979; Trei, 1991), and it occurs in abundance on the shores of western Estonia. Only the *Sphacelaria arctica*–*Polysiphonia fucooides* type microcoenoses, where the biomass of both species is very low, occur at Eru in the Gulf of Finland.

The distribution pattern of the *Cladophora glomerata*–filamentous brown algae microcoenoses and the *Ceramium tenuicorne*–*Furcellaria lumbricalis* microcoenoses (Fig. 4) can be caused by the seasonal variability of dominating annual species. The sampling in the Gulf of Finland was carried out in early

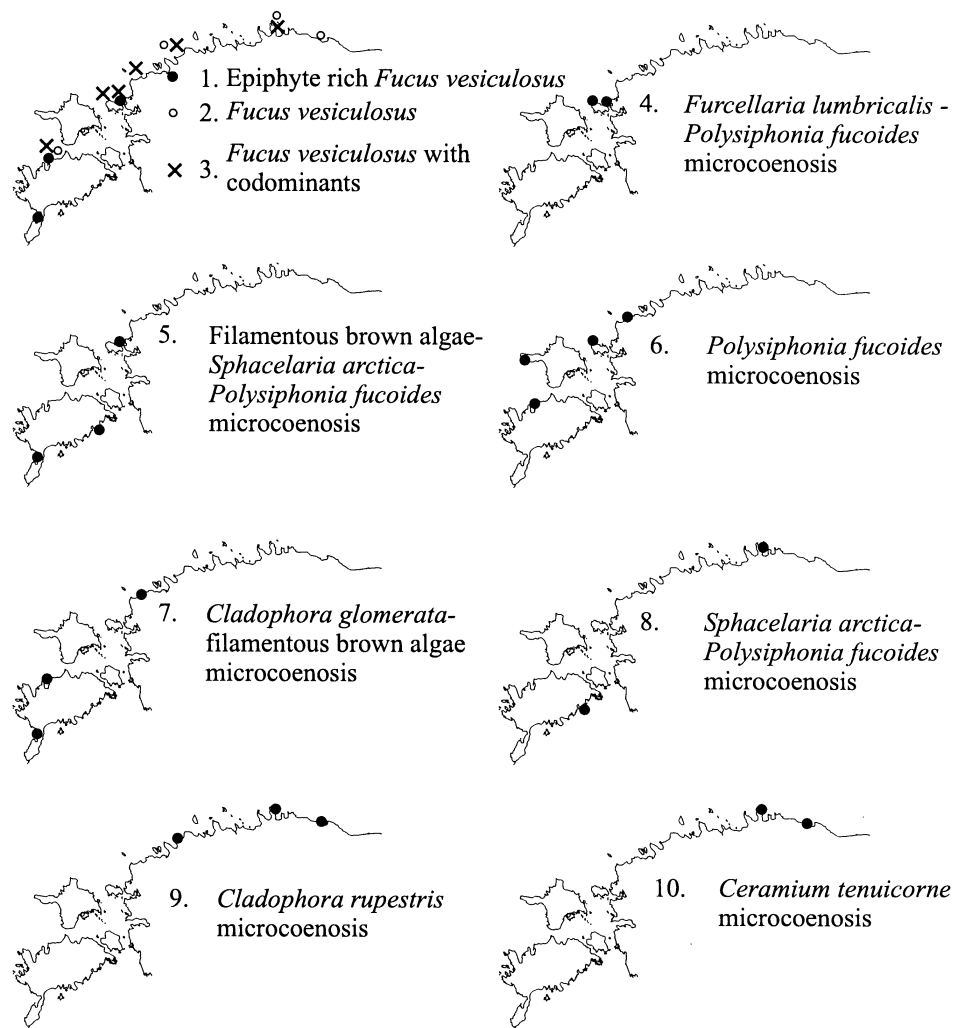


Fig. 4. Distribution of the different types of microcoenoses in the study sites.

October and, in western Estonia, at the end of August. The biomass of the green algae *C. glomerata* is usually declining towards autumn (Kukk, 1979), so the *C. glomerata* dominated areas could no longer be found in October and the low biomass of the *Ceramium tenuicorne*–*Furcellaria lumbricalis* microcoenoses was identified instead. *C. tenuicorne* is one of the most frequent species in the study area, found in small amounts in every studied site, but only in the Eru and Kunda transects did it dominate and form its own microcoenoses.

Dependence of microcoenoses on environmental conditions

According to ANOVA, the largest difference between the microcoenoses of different micro-associations appears in their depth range ($F = 13.4$, $p < 0.001$) (Fig. 5). Microcoenoses of *Cladophora glomerata*–filamentous brown algae, *Cladophora rupestris*, and *Fucus vesiculosus* and *Ceramium tenuicorne*–*Furcellaria lumbricalis* micro-associations are growing in shallow (0.2–3 m) water. The *Sphacelaria arctica*–*Polysiphonia fucoides* type microcoenoses can be found at a depth of 6–8 m. The filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucoides*, *Furcellaria lumbricalis*–*Polysiphonia fucoides*, and *Polysiphonia fucoides* type microcoenoses occur over a large depth range (0.5–11 m).

The difference in substrate hardness between the (micro)habitats of microcoenoses belonging to different types is not significant. Although the study sites were chosen in exposed areas, microcoenoses of some micro-associations differ

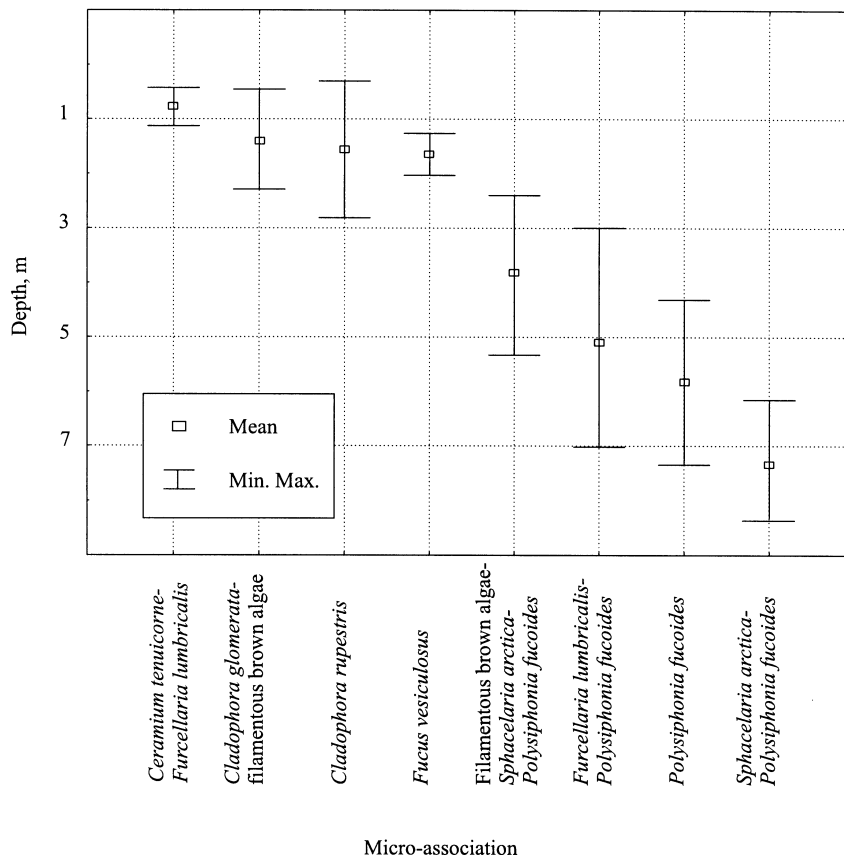


Fig. 5. Growth depth of the different types of microcoenoses. Minimum–maximum and mean depth are shown in every micro-association.

in their exposure range ($F = 7.7$, $p < 0.001$): the microcoenoses of *Furcellaria lumbricalis*–*Polysiphonia fucoides* and the micro-associations of *Polysiphonia fucoides* grow in the most exposed sites, while the filamentous brown algae–*Sphacelaria arctica*–*Polysiphonia fucoides* type microcoenoses occupy more sheltered sites.

Ordination analysis verified the results of the ANOVA and gave a generalized overview of species–environment relations (Fig. 6). The Monte Carlo permutation test confirmed the significance of the first two canonical axes ($p = 0.005$). According to the forward selection procedure, only depth and exposure are statistically significant ($p = 0.005$) environmental factors in describing the species variation (Table 4). Habitat depth is closely related to the first ordination axis. According to that, the red algae *Rhodobryopsis confervoides*, *Coccolithus truncatus*, *Polysiphonia fucoides*, *Ceramium nodulosum*, and *Furcellaria lumbricalis* and the brown algae *Sphacelaria arctica* and *Stictyosiphon tortilis*, growing mainly in deep water, are located on the right side of the ordination plot. *Chara* spp., the brown algae *Chorda filum* and *F. vesiculosus*, the green algae *Cladophora*

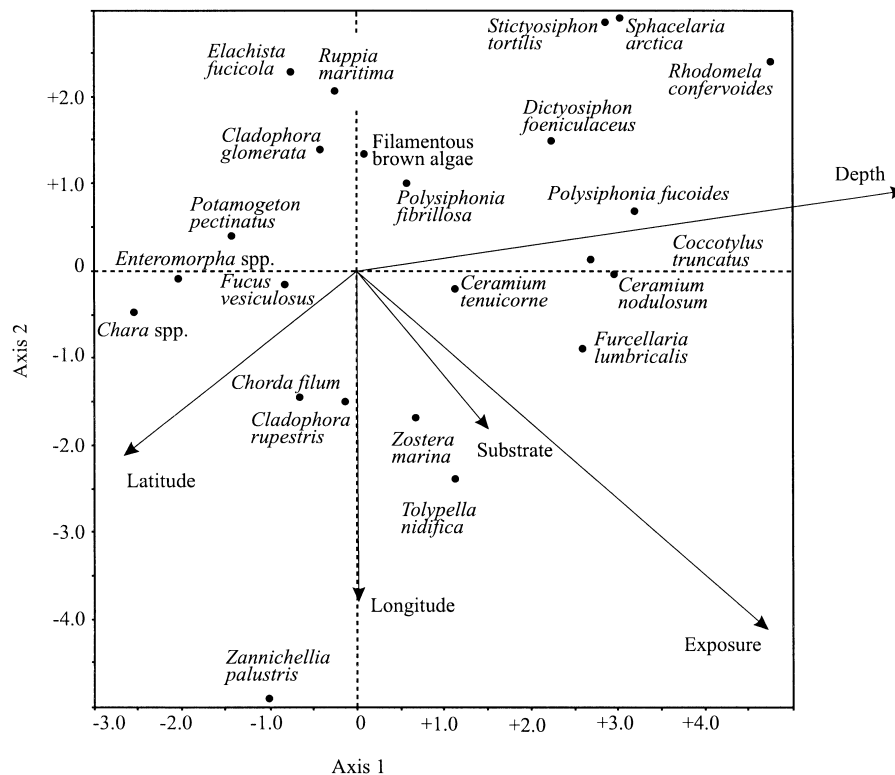


Fig. 6. Ordination biplot of the phytobenthic species and the environmental variables according to canonical correspondence analysis.

Table 4. Conditional effects of the environmental factors according to canonical correspondence analysis. *F* – *F*-criterion, *p* – significance level

Factor	<i>F</i>	<i>p</i>
Depth	8.34	0.005
Exposure	3.25	0.005
Latitude	1.71	0.080
Longitude	1.30	0.215
Substrate	1.13	0.300

glomerata and *Enteromorpha* spp., and the higher plants *Potamogeton pectinatus* and *Zannichellia palustris*, placed at the negative end of the ordination axis, occur in shallow water.

Several environmental factors are related to the second ordination axis. Location of some species is obviously connected with geographic parameters – longitude and latitude, e.g. *Z. palustris*, mainly found from sites in the Gulf of Finland, is situated at the negative end of the axis. Exposure and substrate hardness are related more or less equally to both ordination axes. *Zostera marina* and *Tolypella nidifica*, which are placed towards the positive end of axis one and negative end of axis two, grow in exposed sites on a sandy substrate. *Potamogeton pectinatus*, *Ruppia maritima*, and *Cladophora glomerata* prefer moderately exposed sites.

Many authors (Wærn, 1952; Hällfors et al., 1987; Nielsen & Dahl, 1992) stress the influence of substrate on the heterogeneity of the benthic communities. In the present study the substrate hardness was estimated as average for the whole vegetation belt and not for each 0.2 × 0.2 m square. For that reason the relationship between substrate hardness and heterogeneity of communities does not come to the fore. Moreover, in most of the study area the substrate consisted of a mixture of sand and stones, and the substrate hardness did not differ greatly between the sites.

In their discussion about environmental influences on the species distribution in the Gulf of Riga, Kautsky et al. (1999) emphasized, besides the influence of substrate, the effect of depth. Our findings agree with the results of Kautsky & van der Maarel (1990) from the eastern coast of Sweden, showing that the main environmental factor determining the distribution of benthic vegetation is depth. As discussed above, the transects of the current study were located in areas with similar substrate type (mostly mixed). In different parts of the Gulf of Riga the substrate and water quality conditions are very variable and that is why the substrate appeared to be the most important environmental factor for the phytobenthos (Kautsky et al., 1999). Our study area did not cover the arms of the Gulf of Riga and Gulf of Finland; thus the range of environmental factors was relatively narrow. Still a difference in species composition between open sea areas and gulfs could be detected.

Comparison with previous classifications

In our study the samples were collected only from relatively exposed shores with hard and mixed substrates. Therefore, comparison with previous classifications of phytobenthic communities in Estonia (Trei, 1973, 1991; Kukk, 1978, 1979; Martin et al., 2000) and on the eastern coast of Sweden (Kautsky & van der Maarel, 1990) is relevant only within the limits of similar habitats.

Of the six community types established in the current study, only two (*Fucus vesiculosus* and *Cladophora glomerata* types) are described by all the authors cited in Table 5. It deserves to be noted here that according to Trei (1973, 1991) the community of *Fucus vesiculosus* is the most frequent one in Estonian waters, occurring at depths from 1 to 7 (9) m. In our study the *Fucus vesiculosus*

Table 5. Comparison of current results with other phytobenthic community classifications

Community type	Trei, 1973, 1991	Kukk, 1978, 1979	Kautsky & van der Maarel, 1990	Martin et al., 2000	Current data
<i>Fucus vesiculosus</i>	+	+	+	+	+
<i>Cladophora rupestris</i> – <i>Ceramium tenuicorne</i>	–	–	–	–	+
<i>Cladophora glomerata</i>	+	+	+	+	+
<i>Furcellaria lumbricalis</i> – <i>Polysiphonia fucoides</i>	–	–	–	+	+
Filamentous brown algae – <i>Sphacelaria arctica</i> – <i>Polysiphonia fucoides</i>	+	+	–	–	+
<i>Polysiphonia fucoides</i> – <i>Sphacelaria arctica</i>	+	–	–	–	+
<i>Ceramium tenuicorne</i>	–	–	+	+	–
<i>Cladophora glomerata</i> – <i>Enteromorpha</i> spp.	–	–	–	+	–
<i>Cladophora rupestris</i>	–	–	–	+	–
<i>Enteromorpha</i> spp.	+	+	+	–	–
Filamentous brown algae	+	+	–	+	–
<i>Fucus vesiculosus</i> – <i>Furcellaria lumbricalis</i>	+	+	–	–	–
<i>Furcellaria lumbricalis</i>	+	+	–	+	–
<i>Furcellaria lumbricalis</i> – <i>Ceramium nodulosum</i>	+	–	+	–	–
<i>Furcellaria lumbricalis</i> – <i>Polysiphonia fucoides</i> – <i>Ceramium tenuicorne</i>	+	–	+	–	–
<i>Pseudolithoderma</i> <i>subextensum</i>	+	+	–	–	–
<i>Rhodomela confervoides</i>	–	+	–	–	–

communities were also the most frequent, but their depth range had narrowed considerably, to only 1–3 m. This result can be partly connected with the comparatively limited geographical representativeness and ecological range of the study sites. Still, the community of *Fucus vesiculosus*–*Furcellaria lumbricalis*, found at depths of 6–10 m in earlier studies (Trei, 1973, 1991; Kukk, 1978, 1979), was recorded neither by Martin et al. (2000) nor by us. It seems that while the depth range of *F. vesiculosus* has decreased, the deep-growing community of *Fucus vesiculosus*–*Furcellaria lumbricalis* has disappeared.

The community of *Cladophora rupestris* was noted by Martin et al. (2000), and, as the respective microcoenosis, also in our study, but not earlier by Trei (1973, 1991) and Kukk (1978, 1979). The last two authors described a *Fucus vesiculosus* community with an under-growing layer of *Cladophora rupestris*. *C. rupestris* is probably still growing in the former *F. vesiculosus* area. Nevertheless, this is just a speculation, since there are no observations from exactly the same spots. Large-scale decline of *F. vesiculosus*, documented in different parts of the Baltic Proper (Kangas et al., 1982; Mäkinen et al., 1984; Vogt & Schramm, 1991; Rönnerberg et al., 1995; Schramm & Nienhuis, 1996), has not yet been observed in the eastern Baltic Proper. It was suggested that the reason for the decline of this species was an increase in nutrient concentration, inducing luxurious growth of annual epiphytic algae, which in turn reduces the vitality of *F. vesiculosus* due to competition for light and nutrients (Kangas et al., 1982; Vogt & Schramm, 1991; Schramm & Nienhuis, 1996). In deep water the competition for light is fiercer and therefore *F. vesiculosus* is out-competed first of all in the deeper parts of its distribution area. In the recent study area *F. vesiculosus* has not entirely disappeared, but there are signs of its decline even though our study sites were chosen in the outer parts of bays, representing the conditions without direct land-born nutrient sources. Kukk & Martin (1992) recorded a considerable decrease in *F. vesiculosus* constancy in Pärnu Bay; Kotta et al. (2000) observed the disappearance of *F. vesiculosus* from Kõiguste Bay during 1995–98. Thus the *F. vesiculosus* decline may be more extensive in sheltered sites close to river inputs.

The community type of *Cladophora rupestris*–*Ceramium tenuicorne* has not been described by previous authors, but communities of *Cladophora rupestris* (Martin et al., 2000) and *Ceramium tenuicorne* (Kautsky & van der Maarel, 1990; Martin et al., 2000) have been described separately. In our study the latter two were separated as micro-associations. The community of *Furcellaria lumbricalis*–*Polysiphonia fucoides* has only been described in the present paper and in Martin et al. (2000), not in earlier studies, therefore it is difficult to decide whether we have a true temporal change here, or whether the discrepancies appeared due to the different research methods. The community of *Polysiphonia fucoides*–*Sphacelaria arctica* has only been considered in the present paper and in Trei (1973, 1991).

More than half of the communities listed in Table 5 were not observed in the present paper. The reasons for this could be the narrow amplitude of environmental

conditions covered by the present study and the small number of sampling sites (rare community of *Rhodomela confervoides*). Some of the differences are caused by different sampling methods – for example, the encrusted brown alga *Pseudolithoderma subextensum* did not occur in quantitative samples because it is so tightly attached to stones. The diversity in community names can also be caused by different emphasis put on dominant and character species.

Even though the sampling pattern was not designed for analysing the heterogeneity of communities, it is the first attempt to analyse benthic vegetation on the microcoenoses level in Estonia. Broadening of the study area and the study period would give a better picture of Estonian benthic communities and their mosaic-like pattern, and would test some of the conjectures about distribution presented in this paper.

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Fütobentiliste mikrotsönooside levik Eesti avatud rannikuves

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1998. aasta välihooaja jooksul kogutud biomassiandmete kvantitatiivse analüüsi põhjal on käsitletud Eesti avatud rannikute fütobentilisi mikrotsönoose ja nende levikut mõjutavaid keskkonnafaktoreid. 104 biomassiproovi alusel eristati kaheksa klastrit (mikroassotsiatsiooni). Taimkattevööndite ulatuses keskmistatud andmete põhjal eristus klasteranalüüsil kuus distinktselt koosluse tüüpi. Koosluste mosaiiksuse hindamiseks võrreldi kummalgi tasandil saadud klassifikatsioone. Kõige mosaiiksemaks osutus põisadru (*Fucus vesiculosus*) kooslus, teised kooslused olid märgatavalt homogeensema struktuuriga. Mikrotsönooside lokaalset levikut määravaks peamiseks keskkonnafaktoriks osutus merepõhja sügavus. Enamik mikroassotsiatsioone on piiratud areaaliga, vaid põisadru mikroassotsiatsioon on levinud kogu uurimisalal.