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Impacts of physical environmental characteristics on the distribution of benthic fauna in the northern Baltic Sea

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The Baltic Sea is characterized by steep and strong environmental gradients in physical and chemical parameters which contribute to the geographic distribution of biota. At small scales, uneven bottom topography and heterogeneous sediment features induce high habitat diversity for example in the archipelago areas in the northern Baltic Sea. Here we analyse the impact/importance of sediment types and depth on the distribution of benthic animals in a relatively small (ca. 10 km^2) archipelago area consisting of a mosaic of different benthic habitats interspaced with islands and skerries. A total of 26 major taxa of benthic macrofauna were found/observed in the study area. Results of the CCA analyses where depth and sediment types (clay, mud, sandy silt, fine sand, coarse sand, gravel and stones) were chosen as the environmental factors, revealed that habitat preferences of zoobenthic species were strongly affected by sediment types. Depth also impacted zonation of the species, but did not change the zonation patterns based on sediment characteristics. *Macoma balthica*, *Saduria entomon* and *Harmothoe sarsi* were identified as the only generalists while all other species/taxa showed clear correlation to different sediment types and depth zones. The animal-sediment patterns found reflected largely differential feeding modes of the species. The results clearly showed that sediment characteristics are of decisive importance for the composition of benthic fauna on soft bottoms.

Introduction

Species and the environments they live in are in constant interaction and form a continuum of entities. However, to understand the functioning of marine benthic systems, it is useful to classify the sea floor into distinct habitats. Haskell (1940) gave a broad significance to habitat by defining it as "all things affecting an entity and which it affects at the time in question". While it is recognized that a multitude of factors can potentially contribute to habitat formation, it is also shown that it is often possible to find a few essential environmental variables which determine the distribution of marine benthic fauna (Gray 1974, Freeman and Rogers 2003, Tillin *et al*. 2007). Substratum is useful in defining the habitats of zoobenthos as many benthic species are restricted to certain kind of sediments (Gray 1974).

The benthic fauna in the Baltic Sea consist of a unique combination of marine and freshwater species, with few species specifically adapted to brackish water (Segerstråle 1957, Elmgren 1984). In recent years, more and more invasive species have been introduced into the Baltic Sea e.g. with ballast water, and some of them (such as the polychaete genus *Marenzelleria*) have become established and even dominant in the ecosystem (Perus and Bonsdorff 2004, Bastrop and Blank 2006, Olenin *et al*. 2007). The ecosystem is in rapid change due to excessive nutrient release, climate change and physical habitat destruction. In order to understand and predict dynamics of the marine ecosystem it is important to know how environmental factors shape benthic habitats and communities. The rich mosaic of habitats in the archipelagos of the Baltic Sea may facilitate identification of essential species-environment relationships.

This study analyses how sediment types influence the distribution of soft-bottom zoobenthic species in the sublittoral zone of a diverse archipelago area in the northern Baltic Sea. Furthermore, we studied the relative contribution of bathymetry to sediment types and species distributions. The possible correlation between depth and sediment types was specifically analysed. To decrease the impacts of environmental gradients linked e.g. to oceanography and zoogeography (concerning especially invasive species) occurring at larger geographic scales, this study was conducted at a relatively small scale (ca. 10 km^2) in a coastal archipelago area with high variability in soft-bottom habitats, but relatively stable physical factors such as oxygen and salinity. We hypothesized that despite the low overall species abundance, the small-scale habitat variability would be reflected in the zoobenthos, and hence animal–habitat relationships could be identified.

Material and methods

The study area

The Baltic Sea is geologically young, semi-enclosed, having water exchange only through the shallow and narrow Danish straits, and it is the second largest brackish water basin after the Black Sea (surface area 373 000 km^2). The sea is characterized by strong horizontal and vertical gradients in several oceanographic parameters such as salinity, oxygen content and temperature (Leppäkoski and Bonsdorff 1989, Leppäranta and Myrberg 2009). The coasts of the northern Baltic Sea are in wide areas lined with archipelagoes where the sea bottom consists of topographically complex landscapes. The archipelago area forms a transition zone between the coast and the open sea; factors such as topography, circulation patterns and anthropogenic inputs affect the archipelago ecosystem on a smaller scale compared with coastal or open sea ecosystems (Bonsdorff and Blomqvist 1993, O'Brien *et al*. 2003). Not surprisingly, the fauna of the archipelago is richer than in the open sea area (Bonsdorff and Blomqvist 1993, Bonsdorff *et al*. 2003, O'Brien *et al*. 2003), where it is relatively species poor (Elmgren 1989, Bonsdorff 2006).

The sampling procedures

Samples were taken from 56 benthic stations during 18–26.VII.2007 in the sublittoral zone in the Tvärminne archipelago, at the northwestern coast of the Gulf of Finland (Fig. 1). The area covered about 10 km^2, and the depth range of the sampling stations extended from 4 to 47 meters (Fig. 1). A Van Veen grab, with an area of 0.11 m^2, was used in the sampling.

Sampling sites for the survey were selected prior to sampling, following a stratified random sampling scheme relying on existing information on wave exposure and depth. The entire sampling area was first divided into different strata based on water depth and wave exposure in a geographical information system (GIS) generating random points in each combination of strata consisting of distinct exposure and depth values. The DEM (digital elevation model) used for stratifying depth, was derived by interpolation from nautical chart data. The wave exposure index dataset has been calculated for the coast of Finland using the Simplified Wave Model (SWM) (Isaeus 2004), which calculates expo-

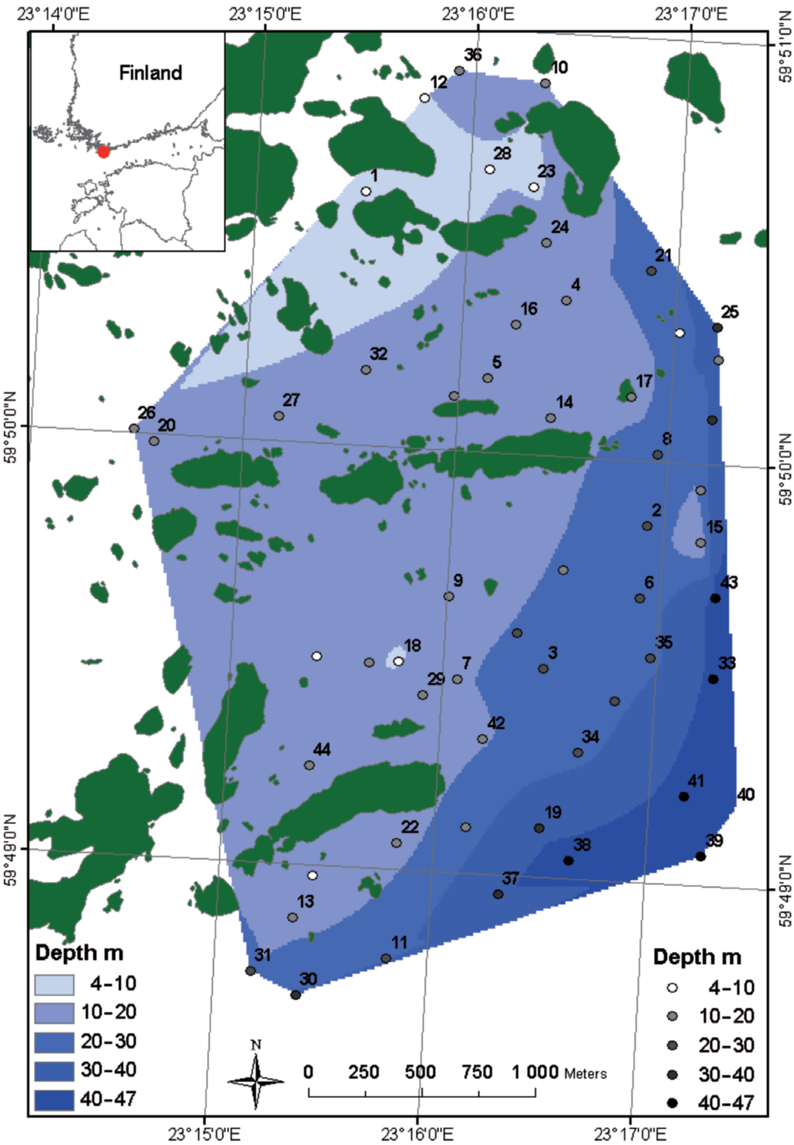

Fig. 1. A bathymetric map of the study area based on the depth at the 56 sampling stations created with the "Natural neighbor" interpolation method. The 44 sampling stations included in the statistical analyses are indicated with numbered dots, while the 12 stations omitted from the analyses are indicated with dots only. The red dot in the index map indicates the study area. Green areas show islands and skerries.

sure from fetch and a 10-year average of wind speed from 16 directions. To reduce spatial autocorrelation between sampling stations an additional criterion of a minimum distance of 200 m between stations was applied in the sampling procedure. One Van Veen grab sample was taken at each station. Due to characteristics of the bottom material, it was impossible to get a quantitative sample from some of the sites. Therefore, a sample was omitted from the analyses, if the volume of sediment in the grab was smaller than 30% of the grab's maximum volume. The volume requirement was set to 30% because most species live in about 15 cm surface layer of the sediment (Rumohr *et al*. 1996), and this would be sufficient for a quantitative sample.

During sampling the sediment types were recorded. The sediment types were defined according to the Wentworth scale (Wentworth 1922), once the sample was emptied into a container from the Van Veen sampler. Additional features used in sediment type identification were colour and smell of the sediments (hydrogen sulfite or not). The animals found were carefully picked on a 1 mm screen when sieving the sediment with sea water. The animals and the sieve residue were preserved in 70% ethanol–water solution. The sieve residue was inspected with a magnifying glass and all animals found were picked. The macrofauna were counted in the laboratory under a dissecting microscope and identified to the species level. Exceptions to this rule were oligochaetes and chironomids, which were identified to the class level, as well as *Hydrobia* spp., *Marenzelleria* spp. and *Pisidium* spp., which were identified to the genus level.

Multivariate statistics and spatial modeling

A multivariate method, constrained correspondence analysis (CCA ordination, later referred to as CCA), was applied to assess the associations between species distributions and spatial environmental variations. CCA is a method suitable for detecting interrelationships of species counts and environmental variables (Palmer 1993, McCune and Grace 2002, Oksanen *et al*. 2006). It is based on χ^2 distances between the selected environmental variables and "dependent" variables (species), and it performs weighted linear mapping (Jari Oksanen, University of Oulu, pers. comm.). In this study, we used CCA to define the occurrence of species in relation to sediment composition and water depth. Prior to CCA the species abundances were log-transformed ($\log_{10}(x + 1)$, where x = number of specimens of a taxon in the sample) to decrease the excessive weight of abundant species over rare species as suggested by e.g. McCune and Grace (2002).

We included only the species present at least at 6% of the stations in the analyses as suggested by Glockzin and Zettler (2008).

The community ecology package "Vegan" (Oksanen *et al*. 2006) programmed with the R language (Ihaka and Gentleman 1996) was used to perform the CCA analyses. After excluding the grab samples with a low sample volume, data from 44 stations were applicable for the CCA analyses.

The environmental data used for the CCA analysis consisted of 7 sediment variables (mud, clay, sandy silt, fine sand, coarse sand, gravel and stones) and water depth from the stations. In the sediment matrix applied in the analyses, each sampling-site-specific vector consisted of the percentage values of the different sediment types.

Glockzin and Zettler (2008) have advised to exclude from the CCA dominant factors which could mask the impacts of some other important explaining factors. We hypothesized that depth could mask the impacts of some other important explaining factors, whereby it could strongly influence the CCA results. Therefore, we conducted three analyses: in the first one, we included the sediment variables and depth as explaining factors for the species/taxa abundance. In the second ordination, we excluded depth from the analysis in order to find out whether exclusion of depth would influence the results and the derived conclusions about impacts of sediment consistency on the abundances of different macrozoobenthos taxa. The third analysis tested only the impact of depth on abundances of zoobenthos.

In order to understand contribution of different environmental factors more profoundly we statistically explored the parameter values associated with the CCA axes. We estimated the significance of each environmental variable as an explanatory factor and the proportional explanatory power of these factors (χ^2) applying permutation tests where the data were permuted randomly and the model was refitted (Jari Oksanen, University of Oulu, pers. comm.).

In order to compare patchiness of occurrence of the species we calculated the coefficient of variation (CV, which is the ratio of the standard deviation to the mean value) for each species. High values of CV (in this study > 4) indicate patchy distribution of a species (Hendricks and Robey 1936).

We produced a depth map based on values from all stations (a total of 56) with interpolation, using the Arc map software (ESRI 1998). We used the "Natural neighbor" interpolation technique to interpolate the depth values. It finds the closest subset of input samples (here 6 stations) to a query point (here cell size equals to 10.64 m) and applies weights to them based on proportionate areas in order to interpolate a value (Sibson 1981).

To visualize the sampling scheme and the distribution of sediment types, we created a map indicating the occurrence and abundance of dominant sediment types in the study area. The map was interpolated, also using the natural neighbor interpolation, based on sediment information from the 44 stations using the Arc map software (ESRI 1998) ver. 9.3.1 (2009). In the sediment map the sites, with even quantity of two or more sediment types, were revealed. The sites were classified according to their sediment composition by giving a value to each specific combination of sediment types; altogether there were 14 different sediment combinations.

Results

Species abundance

Altogether 26 zoobenthic taxa were recorded in the analyses. Due to the applied criteria for low abundance, i.e. the species had to be present at least at 6% of the sampling stations, (Glockzin and Zettler 2008), 18 of the 26 species found were included in the CCA analyses (Table 1). The following species or wider taxa were excluded from the analyses: *Bithynia tentaculata*, *Parvicardium hauniense* and *Pisidium* spp., *Jaera albifrons* and *Asellus aquaticus*, *Cyanopthalma obscura*, *Planaria torva* and insect larvae of the family chironomidae (Table 1).

Table 1. Species found at stations in an ascending order of patchiness (from less patchy to more patchy distribution), their abbreviations, average number of specimen in the samples where they were present, and the coefficient of variation indicating the species patchiness. An asterisk after the taxon name means that it was too rare to be included in the statistical analyses.

Species	Species abbreviation for CCA	Number of CCA stations where observed	Average number of ind./sample	Coefficient of variation	Used in the CCA analyses +/–
Macoma balthica	*Mac bal*	41	104.5	0.83	+
Saduria entomon	*Sadent*	23	5.7	1.40	+
Potamopyrgus antipodarum	*Potant*	26	12.5	1.63	+
Halicryptus spinulosus	*Halspi*	18	4.6	1.67	+
Marenzelleria spp.	*Marenz*	28	64.3	2.23	+
Nereis diversicolor	*Nereis*	10	2	2.25	+
Mya arenaria	*Myare*	13	5	2.42	+
Cerastoderma glaucum	*Cerglau*	8	2	2.59	+
Gammarus oceanicus	*Gamoce*	7	3	2.69	+
Mytilus edulis	*Mytilus*	19	48.6	2.81	+
Harmothoe sarsi	*Harsar*	5	1	2.83	+
Monoporeia affinis	*Monaff*	12	8.1	2.83	+
Gammarus salinus	*Gamsal*	9	8.6	3.18	+
Pygospio elegans	*Pygele*	5	1.8	3.26	+
Oligochaeta	*Oligo*	8	4.9	3.47	+
Hydrobia spp.	*Hydrob*	7	29.1	4.47	+
Theodoxus fluviatilis		3	2.3	4.88	+
Corophium volutator	*Corvol*	5	10.2	4.89	+
*Parvicardium hauniense**		2	1.5	4.90	–
Pisidium spp.*		2	3.5	5.74	–
*Bithynia tentaculata**		2	1	6.63	–
*Jaera albifrons**		0	1.5	6.55	–
*Cyanopthalma obscura**		1	2	7.48	–
*Planaria torva**		0	1	7.48	–
*Asellus aquaticus**		0	1	8.83	–
*Chironomidae**		1	1	8.83	–

There were large differences in species distributions and abundances among the sites (Tables 1 and 2). At many stations there were only one or two abundant species accompanied by few specimens of rare species. *Macoma balthica*, *Saduria entomon*, *Potamopyrgus antipodarum*

Table 2. The depth and sediment type of the 44 sampling stations which were included in the statistical analyses. The three most abundant taxa at each station are given. In some of the sites, however, there were less than three species and in some cases numerous taxa were equally abundant in which case more than the three most abundant taxa are given.

Station	Depth (m)	Sediment type	The most abundant species
1	4.3	95% fine sand, 5% mud	*Potant*, *Cerglau*, *Mya*
2	27.2	85% fine, 15% coarse sand	*Macbal*, *Sadent*, *Halspi*
3	25.1	85% fine, 15% coarse sand	*Macbal*, *Potant*, *Sadent*
4	14.1	50% sandy silt, 50% fine sand	*Macbal*, *Potant*, *Halspi*
5	13.3	75% mud, 15% coarse sand, 5% sandy silt, 5% stones	*Macbal*, *Potant*, *Mya*, *Mytilus*
6	25	50% fine, 45% coarse sand, 5% clay	*Macbal*, *Sadent*, *Marenz*
7	19	50% fine, 50% coarse sand	*Macbal*, *Potant*, *Myare*
8	29.7	85% fine, 15% coarse sand	*Macbal*, *Marenz*, *Sadent*
9	14	45% sandy silt, 45% fine, 5% coarse sand, 5% stones	*Mytilus*, *Macbal*, *Potant*
10	10.6	45% sandy silt, 45% fine sand, 10% stones	*Macbal*, *Potant*, *Mytilus*, *Pisidium*
11	27	45% fine sand, 45% coarse sand, 5% mud	*Macbal*, *Sadent*, *Mytilus*
12	9.4	45% sandy silt, 45% fine, 5% coarse sand, 5% stones	*Macbal*, *Potant*, *Cerglau*
13	15.6	75% coarse, 12.5% fine sand, 12.5% mud	*Mytilus*, *Macbal*, *Mya*
14	14.1	50% mud, 25% fine, 15% coarse sand, 10% gravel	*Macbal*, *Potant*, *Halspi*
15	12.3	85% coarse, 15% fine sand	*Hydrob*, *Mytilus*, *Marenz*
16	12.7	50% coarse sand, 25% sandy silt, 20% fine sand, 5% stones	*Macbal*, *Potant*, *Nereis*
17	12.1	60% sandy silt, 10% mud, 10% fine, 10% coarse sand, 10% gravel	*Macbal*, *Potant*
18	9.3	40% gravel, 40% coarse, 10% fine sand, 10% stones	*Macbal*, *Hydrob*, *Mytilus*
19	38.6	70% clay, 10% mud, 10% coarse, 10% fine sand	*Macbal*, *Marenz*, *Monaff*
20	11.8	40% mud, 40% sandy silt, 10% fine sand, 10% gravel	*Macbal*, *Potant*, *Marenz*
21	24.3	70% mud, 25% sandy silt, 5% fine sand	*Macbal*, *Marenz*, *Mytilus*
22	16	45% mud, 45% gravel, 5% coarse, 5% fine sand	*Mytilus*, *Macbal*, *Corvol*
23	8.1	95% sandy silt, 5% coarse sand	*Macbal*, *Myare*, *Cerglau*, *Nereis*
24	15.2	50% sandy silt, 25% coarse sand, 25% stones	*Macbal*, *Potant*, *Hydrob*, *Marenz*
25	34.9	50% sandy silt, 25% mud, 10% coarse sand, 10% gravel, 5% stones	*Macbal*, *Marenz*, *Halspi*
26	11	75% mud, 12.5% sandy silt, 12.5% gravel, 5% clay	*Macbal*, *Potant*, *Mytilus*
27	11.8	45% sandy silt, 45% fine sand, 5% gravel, 5% coarse sand	*Macbal*, *Nereis*
28	9.2	50% gravel, 30% stones, 10% sandy silt, 10% mud	*Macbal*, *Potant*, *Halspi*
29	16.2	45% stones, 45% coarse, 5% fine sand, 5% gravel	*Macbal*, *Mytilus*, *Myare*
30	30.8	40% clay, 30% gravel, 30% stones	*Macbal*, *Halspi*, *Sadent*
31	21.2	40% clay, 30% gravel, 30% stones	*Macbal*, *Mytilus*, *Potant*
32	12.2	75% mud, 12.5% clay, 12.5% gravel	*Marenz*
33	42.3	85% mud, 10% gravel, 5% clay	*Marenz*, *Macbal*, *Monaff*
34	27.5	50% clay, 50% coarse sand	*Macbal*, *Marenz*, *Halspi*
35	27.1	50% clay, 45% coarse, 5% fine sand	*Macbal*, *Marenz*, *Halspi*, *Monaff*
36	14.8	80% mud, 15% coarse sand, 5% clay	*Macbal*, *Potant*
37	39.3	70% clay, 25% mud, 5% coarse sand	*Macbal*, *Marenz*, *Monaff*
38	42.5	95% clay, 5% mud	*Marenz*, *Macbal*, *Monaff*
39	46.1	95% mud, 5% clay	*Marenz*, *Macbal*
40	47.1	95% mud, 5% clay	*Marenz*
41	43.1	95% mud, 5% clay	*Marenz*, *Macbal*, *Sadent*
42	18.7	85% mud, 15% clay	*Macbal*, *Marenz*, *Potant*
43	42.2	95% mud, 5% clay	*Macbal*, *Marenz*, *Monaff*
44	14.2	95% mud, 5% clay	*Marenz*, *Nereis*

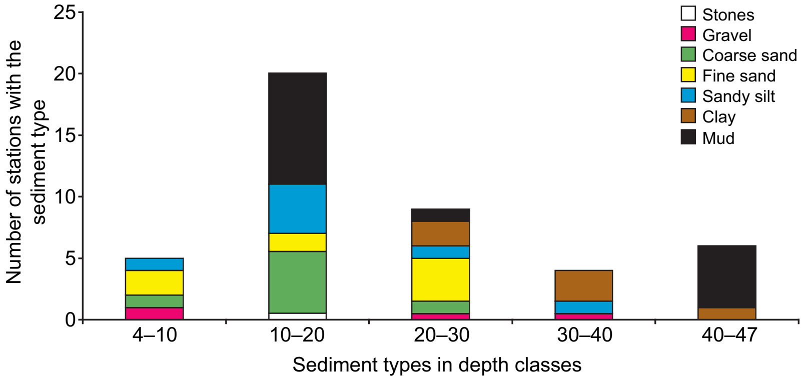

Fig. 2. Frequency of sediment types in 5 depth classes (4–47 m).

and *Marenzelleria* spp. were the most common species (Table 1). *Macoma balthica* was also the most abundant species in the samples (Tables 1 and 2) and it was evenly distributed among the stations. Also *Saduria entomon*, although at lower abundances than *Macoma balthica*, was evenly distributed among the stations. In general, there were several species at each station, while at few stations there were only one or two species present. *Marenzelleria* spp. often appeared alone or with only one other species in low abundance. *Potamopyrgus antipodarum* often occurred at high abundances accompanied by *Macoma balthica* (Tables 1 and 2). *Hydrobia* spp. had a patchy distribution. *Marenzelleria* spp., which favored muddy deeper bottoms, was neither a generalist nor patchily distributed but both *Marenzelleria* spp. and *Mytilus edulis* were often very abundant at sites where they occurred. Some species, such as *Cerastoderma glaucum*, *Mya arenaria*, *Harmothoe sarsi* and *Theodoxus fluviatilis* occurred patchily, but were low in numbers (Table 1).

Species distribution according to sediment types and depth

Mud was the most common sediment type at the sampling stations, followed by fine sand, clay and sandy silt. Clay occurred in deeper parts of the study area, mud in medium depths and deep sites and gravel and coarse sand on shallower sampling sites (Table 2 and Figs. 1–3).

The two CCA models (with "sediment types" and with/without "depth" as a component) showed similar general patterns, indicating the distribution of species in relation to the different sediment types (Figs. 4 and 5). The component axes resulting from the CCA reflected the gradients in species proportions constrained by the environmental variables (Makarenkov and Legendre 2002) (8 in the first analysis, 7 in the second analysis and 1 in the third analysis). The axis one, being parallel with depth (the first and third analysis), clay and mud (the second analysis) explained most of the variation by the constrained axes (Tables 3 and 4).

Species distributions were clearly linked to distinct sediment types (Figs. 4 and 5). In addition depth was an important driving factor for the following species: *Marenzelleria* spp. and *Monoporeia affinis* (which correlated positively with depth) and *Cerastoderma glaucum* (which correlated negatively with depth) (Table 5 and Fig. 6). *Marenzelleria* spp. and *Monoporeia affinis* mainly appeared in clay and mud dominated sediments and *Halicryptus spinulosus* in soft clay dominated sediments. The majority of the species appeared in mixed to coarse sediments. The gastropods *Hydrobia* spp. and *Potamopyrgus antipodarum* were primarily found in sediments dominated by fine sand and sandy silt. The polychaete *Pygospio elegans*, the amphipod *Corophium volutator*, oligochaeta, the bivalve *Mya arenaria* and the gastropod *Theodoxus fluviatilis* preferred sediments primarily dominated by coarse sand. The bivalves *Mytilus edulis* and *Cerastoderma glaucum*, the polychaete *Nereis diversicolor* and the amphipods *Gammarus salinus* and *G. oceanicus* occurred mainly on stony to gravelly sediments and correlated negatively

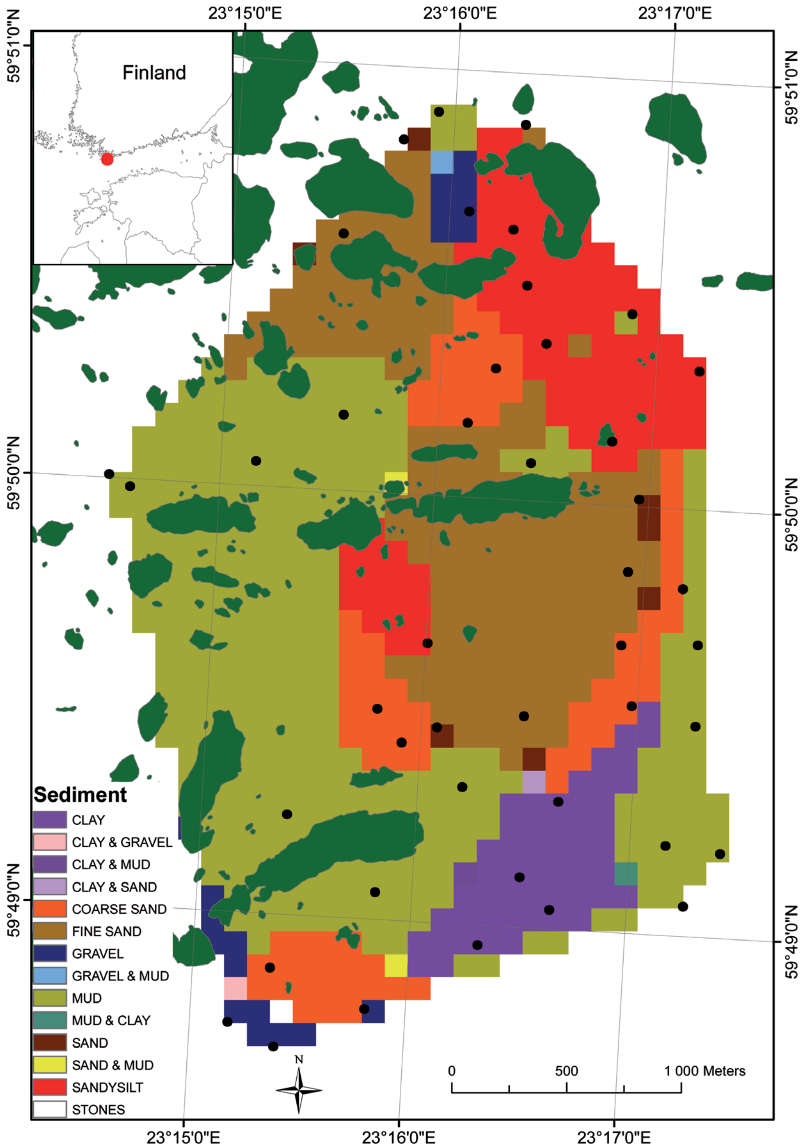

Fig. 3. Distribution of distinct sediment types in the study area, based on the 44 stations included in the statistical analyses, created with the "Natural neighbor" interpolation method. The 14 different sediment categories result from combinations (with even abundances) of distinct sediment types at the sampling sites. The red dot in the index map indicates the study area. Green areas show islands and skerries.

with clayey sediment. The bivalve *Macoma balthica*, the isopod *Saduria entomon* and the polychaete *Harmothoe sarsi* were generalists when it came to sediment and were not related to any specific depth zone.

In the second CCA analysis in which depth was excluded, the explanatory power of distinct sediments differed only in minor details from the first CCA ordination (Table 4 and Fig. 5). Also the third CCA analysis with only depth as an environmental variable significantly explained species distribution, although it did not explain as much of the variation in species occurrence as the analyses with both depth and sediment types or only sediment types as environmental variables (Table 5). Depth seemed to be of major importance for some of the species but for most of the species it wasn't the driving force (Fig. 6). When comparing the analyses with and without depth as a factor it became evident that sediment types were the main driving factor for species distribution.

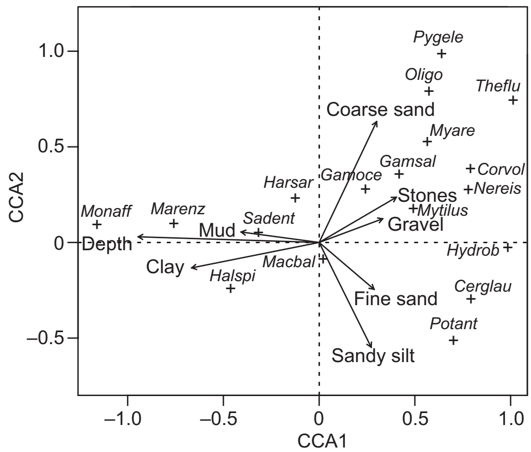

Fig. 4. The CCA analysis depicting the relationships between zoobenthos, sediment types and depth.

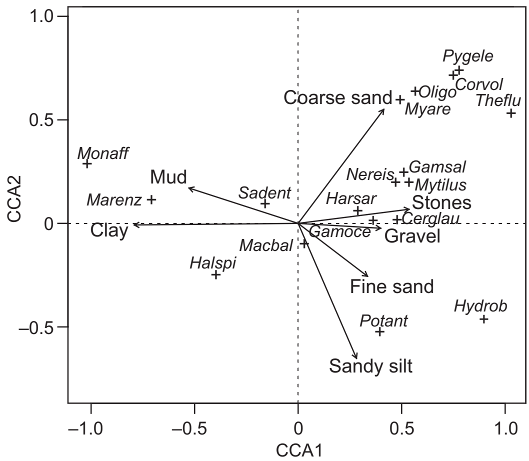

Fig. 5. The CCA analysis depicting the relationships between zoobenthos and sediment types, excluding depth.

Discussion

Relationships between zoobenthic species and sediment types

Our study shows clearly that the local spatial variation of seabed sediment structure is to a large part responsible for the variation in distribution of macrozoobenthos. Thus, our results agree with recent findings in studies in the southern Baltic Sea (Glockzin and Zettler 2008, Gogina *et al*. 2010), that have stressed the importance of sediment grain size, i.e. sediment

Table 3. The CCA analysis with sediment types and depth included as environmental factors. The proportion of variance (inertia) explained by the axes in total and by constrained and unconstrained axes separately. In addition, the proportion of variance explained by the three first constrained (CCA) axes. The Permutation tests for depth, sediment types and related CCA -axes including degrees of freedom (df), the explanatory power of the variables (χ^2) and the statistical significance value (p).

Inertia total = 1.35, constrained = 0.53, unconstrained = 0.81			
	df	χ^2	*p*
Model	8	0.60	0.005**
Residual	35	0.90	
CCA1	1	0.31	0.005**
CCA2	1	0.08	0.300
CCA3	1	0.05	0.850
Depth	1	0.10	0.005**
Mud	1	0.09	0.015*
Clay	1	0.15	0.005**
Sandy silt	1	0.04	0.195
Fine sand	1	0.05	0.085
Coarse sand	1	0.05	0.060
Gravel	1	0.03	0.300
Stones	1	0.03	0.290

Table 4. The CCA analysis with only sediment types included as environmental factors. The proportion of variance (inertia) explained by the axes in total and by constrained and unconstrained axes separately. In addition, the proportion of variance explained by the three first constrained (CCA) axes. The permutation tests for sediment types and related CCA axes including degrees of freedom (df), the explanatory power of the variables (χ^2) and the statistical significance value (p).

Inertia total = 1.35, constrained = 0.45, unconstrained = 0.90			
	df	χ^2	*p*
Model	7	0.45	0.005**
Residual	36	0.90	
CCA1	1	0.24	0.005**
CCA2	1	0.08	0.170
CCA3	1	0.04	0.89
Mud	1	0.09	0.010*
Clay	1	0.15	0.005**
Sandy silt	1	0.04	0.240
Fine sand	1	0.05	0.100
Coarse sand	1	0.05	0.115
Gravel	1	0.03	0.345
Stones	1	0.04	0.185

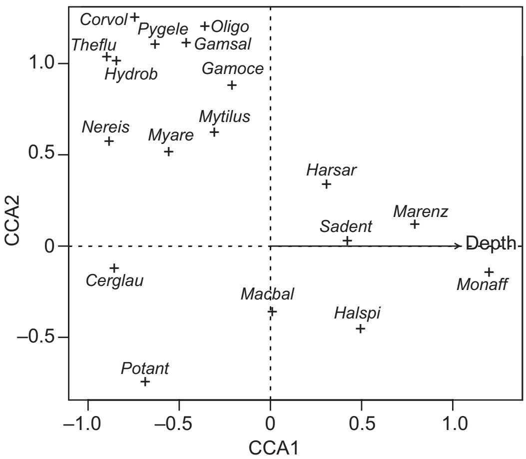

Fig. 6. The CCA analysis depicting the relationships between zoobenthos and depth.

type, as an important factor shaping zoobenthic communities. Pellegrino and Hubbard (1983), as cited in Zajac *et al*. (2000), found that species richness differed significantly among sedimentary habitats and that higher numbers of species were found in areas of sediment sorting than in areas of sediment transport or deposition. In this study, we found a similar pattern in the species distribution in relation to sediments. Also depth impacts the species distribution. Although depth would not in itself be an environmental feature responsible for the species distribution, factors, such as salinity, oxygen, temperature and sediment types, that determine the suitability of a habitat for a certain species often correlate with depth (Gogina *et al*. 2010) because depth controls many physical, chemical and ecological processes in the benthic ecosystem (Zajac *et al*. 2000). Depth can thus be used as a proxy for oceanographic parameters such as salinity, oxygen content and temperature, or other dynamic factors associated with depth, which would need continuous recording in such dynamic environments as the Baltic archipelagoes (Bonsdorff and Blomqvist 1993).

Table 5. The CCA analysis with only depth included as an environmental factor. The proportion of variance (inertia) explained by the axes in total and by constrained and unconstrained axes separately. In addition, the proportion of variance explained by the constrained axis (CCA) and by the two unconstrained axes (CA). The permutation tests for depth and related CCA axis including degrees of freedom (df), the explanatory power of the variables (χ^2) and the statistical significance value (p).

Inertia
total = 1.34, constrained = 0.31, unconstrained = 1.03

	df	χ^2	p
Model	1	0.31	0.005**
Residual	36	1.03	
CCA1	1	0.31	0.005**
CA1		0.30	
CA2		0.14	
Depth	1	0.31	0.005**

Part of the spatial variation of zoobenthos caused by sediment structure may be affected by differential food consistency and processes that occur within the benthic habitats (Tillin *et al*. 2007). Rodil *et al*. (2009) found that surface and subsurface deposit feeders dominated in the sand and muddy sand, and highly motile carnivores in coarse sediments. Further, they found that deposit feeders were more abundant in fine grained sediments which contained more organic matter. Those observations were partly supported by this study, i.e. suspensivores and deposit feeders such as *Monoporeia affinis* and *Marenzelleria* spp. were found in soft sediments which potentially contain a lot of organic material and an omnivorous carnivore *Nereis diversicolor* occurred in coarser sediments with potential prey species present. The carnivores *Saduria entomon* and *Harmothoe sarsi* were not, however, selective of sediment types. The predatory priapulid *Halicryptus spinulosus* was found in soft sediments. Distribution of *Halicryptus spinulosus* is probably also associated with the occurrence of favorable prey items in the soft bottom environment (Aarnio *et al*. 1998). In addition we observed that the filter feeders such as *Cerastoderma glaucum* and *Mya arenaria* and grazers such as *Gammarus* spp. occurred in coarse sediments. *Macoma balthica* was found to be a generalist concerning sediment types in contradiction to the study by Gogina *et al*. (2010) who found a high positive correlation between abundance and sediment parameters for *Macoma balthica*. Ólafsson (1986) and Nordström *et al*. (2009) concluded that *Macoma balthica* can switch feeding modes depending on sediment type, and hence it can adapt to any kind of soft sediment. Furthermore, Beukema (1993) discovered that the habitat preference of *Macoma balthica* varies according to the best adaptive strategy for the different life stages (i.e. size classes), which has also been illustrated from the Baltic Sea by Bonsdorff *et al*. (1995).

It is evident that depending on the spatial scale, the weights of distinct explanatory factors for species distribution patterns vary (Hewitt *et al*. 2007). In the current study, the conclusions concerning environmental impacts on species distribution relied on sampling within a relatively small spatial scale (ca. 10 km^2), which enabled detailed analyses of the effects of bathymetry and sediment type on zoobenthos abundance, while oceanographic variations can be expected to be less important than in wider scales. In the wide scale of the entire Baltic Sea, also oceanographic features such as salinity and temperature are important determinants of the distribution of the most characteristic macrozoobenthic species (Bonsdorff and Pearson 1999, Gogina and Zettler 2010) and in those scales even relatively rough spatial estimates of oceanographic variables may enable determining the impacts of those factors on species abundance. Spatial patterning of benthic fauna is likely to be a combination of factors such as sediment composition, successional state of the ecosystem, spatial variation in recruitment, or interspecific interactions (Legendre *et al*. 1997) and gradients on a large scale can appear as patchy patterns on a small scale (Levin 1992). The effects of biotic interactions on species distribution are manifested on the smallest spatial scales from centimeters to meters and at larger scales the environmental factors become dominant in shaping species patterns (Zajac *et al*. 1998, Bergström *et al*. 2002). The structure of the environment is not only scale dependent but is also affected by the structural configuration of the environment. In the open sea, especially at exposed areas, the role of currents as forming species patterns is larger than at sheltered sites (Valanko *et al*. 2010), such as inner archipelago areas. Further, the macro-environmental hydrographic gradient naturally sets boundaries for species distribution (Bonsdorff 2006).

It is likely that species-specific differences in colonization histories and in the ability to re-colonize had smaller impacts on the scales of the current study compared with those of studies where sampling was performed over wider sea areas (Zajac *et al*. 1998). Generally, in shallow coastal areas the severe environmental conditions cause the organisms to experience more variable population patterns than do organisms of deeper areas (Bonsdorff and Pearson 1999).

Zoobenthos–depth linkage

The species observed in this study can be clearly classified as shallow water (about 4–10 meters) and deeper sublittoral (about 10–47 meters) organisms. Deposit feeders and predators, such as *Marenzelleria* spp., *Monoporeia affinis* and *Halicryptus spinulosus* seem to thrive optimally in slightly deeper parts, and filter feeders such as *Cerastoderma glaucum* and grazers such as *Gammarus* spp. at shallower depths. This is in line with the findings of Glockzin and Zettler (2008) and Aarnio *et al*. (2011).

Sensitivity of the Baltic Sea stresses the importance of biodiversity and monitoring of changes

The Baltic Sea is subject to severe environmental degradation due to human activities. The Gulf of Finland has become one of the most eutrophic areas within the Baltic Sea (HELCOM 2009). The archipelago areas constitute important zones for maintenance of biodiversity and marine ecosystem functions. Assessing the biodiversity of a sea area is important in marine environmental protection and allows us to get information on invasive species and their impacts on ecosystems. It is also a basis for ecosystem restoration.

Knowledge of how and by which factors biotic entities are shaped and application of spatial modeling tools provide possibilities to understand and map biodiversity, support effective conservation and restoration of marine areas as well as enable sustainable use of renewable marine resources (Galparsoro *et al*. 2010). Mapping of habitats and their components may enable us to understand where certain species are found and why. Sediment types can efficiently be classified over large areas with remote sensing using hydroacoustics (Hellequin *et al*. 2003, Solan *et al*. 2003) in combination with grab sample information on sediment quality (Galparsoro *et al*. 2010).

The knowledge of marine systems is often based on information collected from selected sites that are unable to give a holistic view of the benthic ecosystem. Current modeling studies using GIS-based methods and multivariate methods such as CCA, allow us to understand patterns of abiotic and biotic components of the ecosystems in an efficient way. This study clearly shows that at least over small to moderate landscape scales the link between sediment character/type and zoobenthos is a valid descriptor and should be acknowledged/taken into account in assessing biodiversity and management options for coastal areas.

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