Important scales of distribution patterns of benthic species in the Gretagrund area, the central Gulf of Riga

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Abstract. In this paper we quantify the relative importance of scale-specific variability of the prevalent macroalgal and benthic invertebrate species in the Gretagrund area, the central Gulf of Riga. The spectra of variability were related to those of different abiotic environmental factors. The used methodology allows identifying the correlation scales in which environmental variability predicts the distribution of benthic communities. The study showed that the spatial variability of benthic macrophytes and invertebrates varied among species and there was no key single spatial scale where the variability of species was higher. The study also showed that multiple environmental variables interactively contributed to the spatial patterns of benthic macrophyte and invertebrate species.

Key words: Baltic Sea, benthic invertebrates, macrophytes, nonindigenous, patterns, spatial scale.

INTRODUCTION

Spatial variability in the marine environment can occur on a wide range of scales. To date, the knowledge about the relative importance of scale-specific variability on marine ecosystems is practically lacking. It was not until recently that scientists started to quantify the spatial patterns of a single abiotic (seawater temperature, coastal topography) or biotic variable (e.g. chlorophyll *a*, cover estimate of a species, diversity) (Denny et al., 2004). Despite these developments there is still an urgent need for empirical tests of important scales of environmental factors and biological patterns at different ecosystems and habitats.

Fundamental research questions have generally been studied experimentally from the scales of centimetres to metres and we are aware which mechanisms are behind the local patterns (see e.g. Kotta et al., 2008a for references about the north-eastern Baltic Sea). However, much less is known about how the larger-scale environmental and biotic variability directly and indirectly affects species at a site scale (Hewitt et al., 2007; Kotta et al., 2008b; Kotta & Witman, 2009). The studies that relate the spatial patterns of environment and species at a multitude of

scales help us to unveil factors and processes generating biotic patterns through all the studied scales.

In this paper we quantify the relative importance of scale-specific variability of the prevalent macroalgal and benthic invertebrate species. The spectra of variability are related to those of different abiotic environmental factors. Following Steele & Henderson (1994), we assumed that if environmental variables had large effects on communities at certain spatial scales then these communities would have high spatial variance at this scale.

MATERIAL AND METHODS

The Gulf of Riga is a wide, shallow, semi-enclosed brackish water ecosystem of the northern Baltic Sea. The gulf receives fresh water from a huge drainage area (134 000 km^2), mostly entering the southern part of the basin. The average salinity varies from 0.5–2.0 in surface layers in its southern and northeastern areas to 7 at the straits. In most parts, however, the salinity is 5.0–6.5 and there is no permanent halocline. Because of its shallowness, the dynamics of both surface and deep water temperatures is directly linked to air temperatures. The oxygen regime is relatively good due to strong vertical mixing. The gulf is on average twice as eutrophicated as the Baltic Proper, and the outflow of nutrients through the straits is higher than the inflow (Kotta et al., 2008a and references therein).

The study was conducted in the central Gulf of Riga in May 2008 in the frame of the habitat mapping of 'Inventory of benthos and habitats in the Gretagrund area' coordinated by the Estonian Fund for Nature. The average depth of the study area was 17 m with a maximum of 39 m. Sand, gravel, or pebble bottoms dominated. The phytobenthos and associated benthic invertebrate sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE programme (HELCOM, 2006). The sampling was performed by an Ekman type bottom grab (400 cm^2). A total of 83 stations were sampled and three replicate samples were taken in each station (Fig. 1).

Sediment samples were sieved through a 0.25 mm mesh and the residuals were preserved in a deep freezer at −20 °C. In the laboratory, plants and animals were counted and identified under stereo dissecting microscope. Dry weights of all taxa were obtained after keeping the material for 2 weeks at 60 °C.

A simplified Wave Model method was used to calculate the wave exposure for mean wind conditions represented by the ten year period between 1 January 1997 and 31 December 2006 (Isæus, 2004). A nested-grids technique was used to ensure long distance effects on the local wave exposure regime. The resulting grids had a resolution of 25 m.

Multivariate data analyses were performed by the statistical program 'PRIMER' version 6.1.5 (Clarke & Gorley, 2006). Similarities between all pairs of samples were calculated using a zero-adjusted Bray–Curtis coefficient. The coefficient is known to outperform most other similarity measures and enables samples containing no organisms at all to be included (Clarke et al., 2006). The software
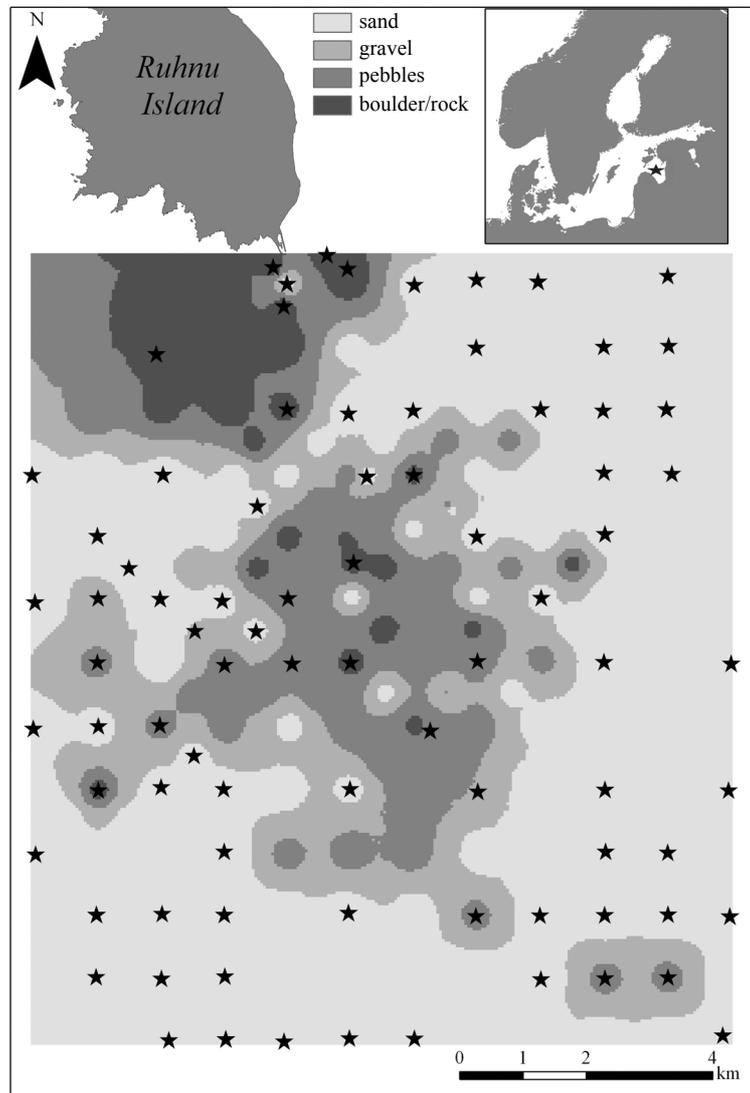
Fig. 1. Study area. The star in the upper right map denotes the location of the Gretagrund shallow in the Gulf of Riga. Sampling stations are indicated by stars. Sediment characteristics are shown.

ArcInfo (Anon., 2004) was used to calculate the point distances between the studied sites. The point distances were related to the dissimilarity matrices of environment and biota. The distance-based mean dissimilarities were used as a proxy of the scale-specific spatial variability of abiotic environment and biota. Multiple regression analysis with Statistica version 8.0 was used to seek which abiotic environmental variable describes the best the observed biotic patterns (StatSoft, 2008). An ArcInfo kriging tool was used to generate an estimated surface of species distributions from a scattered set of points.

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RESULTS AND DISCUSSION

Altogether 47 taxa were identified in the study area. Among these 36 were benthic invertebrate species and 11 were benthic macrophytes (Tables 1, 2). For the first time we identified *Paramysis intermedia* in the Baltic Sea area. The species is known to be indigenous to the Ponto-Caspian region (Audzijonytea et al., 2008) and was found just occasionally at one station.

Table 1. Average biomasses, occurrence (% of findings), and depth range of zoobenthos taxa in the Gretagrund area

Taxon	Average biomass per stations, g m^{-2}	Occurrence, %	Min depth, m	Max depth, m
Balanus improvisus Darwin	6.60	38.2	2.1	22.2
Bathyporeia pilosa Lindström	0.01	5.6	10.3	15
Cerastoderma glaucum (Poiret)	0.39	9.0	11	20
Chironomidae	<0.01	5.6	2.1	7.3
Cordylophora caspia (Pallas)	<0.01	1.1	9	11
Corophium volutator (Pallas)	0.01	16.9	2.1	28
Diptera	<0.01	1.1	13	13
Dreissena polymorpha (Pallas)	0.01	1.1	11	11
Electra crustulenta (Pallas)	<0.01	1.1	10	10
Gammarus juv. Fabricius	<0.01	9.0	2.1	19
Gammarus oceanicus Segerstråle	2.60	1.1	2.1	2.1
Gammarus salinus Spooner	<0.01	4.5	2.1	7.3
Gammarus zaddachi Sexton	0.02	5.6	2.1	17
Halicryptus spinulosus von Siebold	0.03	3.4	25	39
Hediste diversicolor (O. F. Müller)	0.01	15.7	5.4	38.2
Hemiptera	<0.01	1.1	34.2	34.2
Hydrobia ulvae (Pennant)	0.01	11.2	2.1	25
Idotea balthica (Pallas)	0.03	5.6	2.1	9
Idotea chelipes (Pallas)	0.01	3.4	2.1	6.3
Idotea granulosa Rathke	<0.01	1.1	2.1	2.1
Jaera albifrons Leach	<0.01	6.7	5.6	12
Laomedea flexuosa Alder	<0.01	2.2	6.3	34.2
Leptocheirus pilosus Zaddach	<0.01	6.7	2.1	17
Lymnea peregra (Müller)	0.01	4.5	4.9	4.9
Macoma balthica (L.)	15.13	58.4	5.4	39
Marenzelleria neglecta (Sikorski et Bick sp. nov.)	<0.01	18.0	5.4	34.2
Melita palmata (Montagu)	<0.01	1.1	13	13
Monoporeia affinis (Lindström)	0.44	12.4	17.7	34.6
Mya arenaria L.	0.07	4.5	13.4	19.1
Mytilus trossulus Gould	4.30	40.4	2.1	26
Oligochaeta	0.03	34.8	5.4	34.2
Paramysis intermedia (Czerniavsky)	<0.01	1.1	2.1	2.1
Pontoporeia femorata Krøyer	<0.01	2.2	29	34.5
Saduria entomon (L.)	0.06	4.5	26	34.2
Theodoxus fluviatilis (L.)	0.62	16.9	2.1	19.5
Trichoptera	<0.01	2.2	5	5.6

Table 2. Average biomasses, occurrence (% of findings), and depth range of macrophyte species in the Gretagrund area

Species	Average biomass, per stations, g m^{-2}	Occurrence, %	Min depth, m	Max depth, m
Ceramium tenuicorne (Kützing) Waern	0.41	10.1	2.1	12
Ceramium virgatum Roth	<0.01	3.4	7.3	7.3
Cladophora glomerata (L.) Kützing	0.04	11.2	2.1	7.3
Cladophora rupestris (L.) Kützing	<0.01	1.1	5.6	5.6
Fucus vesiculosus L.	3.48	1.1	2.1	5.6
Furcellaria lumbricalis (Hudson) J. V. Lamouroux	0.10	2.2	8	11
Pyaiella littoralis (L.) Kjellman	0.75	5.6	2.1	6.3
Polysiphonia fucoides (Hudson) Greville	0.05	5.6	4.9	12
Polysiphonia fibrillosa (Dillwyn) Sprengel	<0.01	1.1	4.9	12
Rhodomela confervoides (Hudson) P. C. Silva	0.01	1.1	9	9
Sphacelaria arctica Harvey	0.16	23.6	4.9	13

The distribution pattern varied among prevailing species. Because of low water transparency macrophyte assemblages were poorly developed in the study area and only two species – *Polysiphonia fucoides* and *Sphacelaria arctica* – were found at extensive areas in the Gretagrund shallow. These macrophyte species had patchy distribution with *P. fucoides* having highest biomasses in the western part and *S. arctica* in the central part of the study area. Other macrophyte species were distributed in the vicinity of Ruhnu Island. *Macoma balthica* was by far the most dominant benthic invertebrate species in the Gretagrund area. The highest biomasses of the species were observed in the south-western and north-eastern parts of the study area. Similarly to the prevalent macroalgal species, *Mytilus trossulus* and *Balanus improvisus* had patchy distribution with higher biomasses in the central and south-eastern study areas (Figs 2, 3).

The dissimilarities of species biomasses were ordered by the spatial distance between stations. Such analysis gave us the spatial variability patterns of the species. Based on the spatial variability patterns five groups of benthic macrophytes and invertebrates were identified (Fig. 4). *Polysiphonia fucoides* had low biomass variability at all studied scales with occasional random small peaks. The variability of *M. balthica* increased curvilinearly up to 4 km spatial scale and then levelled off. The biomass variability of *S. arctica*, on the contrary, was high at smaller spatial scales, declining with increasing scale up to 8 km. At larger spatial scales relatively low and constant biomass variability was observed. Both *M. trossulus* and *B. improvisus* had high and relatively constant spatial variability at spatial scales up to 6–7 km. Above this scale the spectrum showed a distinguished depression but further away the spatial variability increased again.

It has been suggested that if environmental variables have large effects on macrophytes and invertebrates at certain spatial scales, then macrophyte and invertebrate biomasses have high spatial variance, i.e. their biomasses are dissimilar at this scale (Steele & Henderson, 1994). Thus, different spatial variability patterns observed
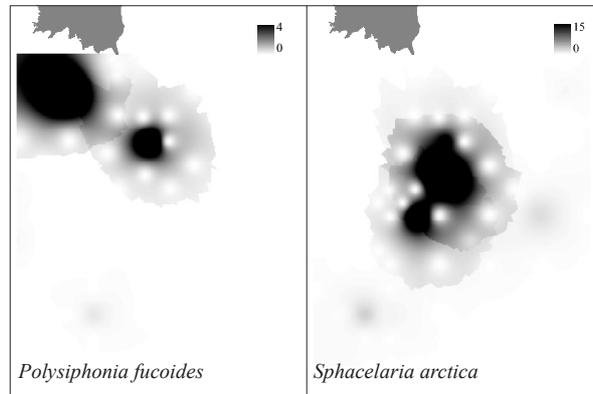
Fig. 2. Distribution of biomasses of the prevalent benthic macrophyte species in the Gretagrund area (dw g m^{-2}). An ArcInfo kriging tool was used to generate an estimated surface of species distributions from a scattered set of points.
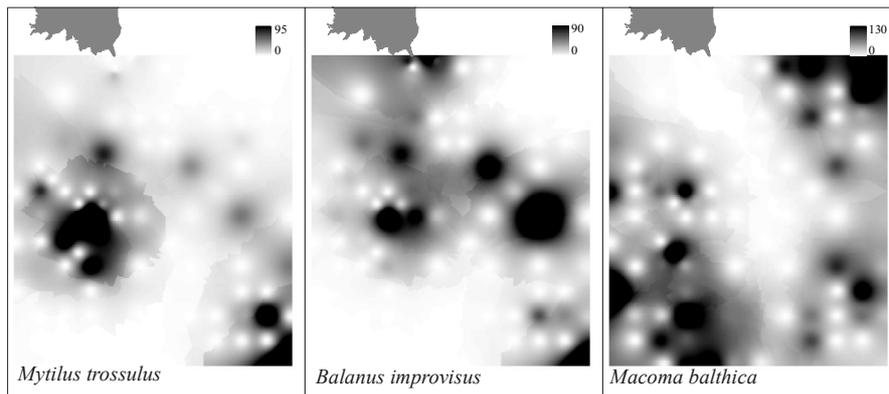

Fig. 3. Distribution of biomasses of the prevalent benthic invertebrate species in the Gretagrund area (dw g m^{-2}). An ArcInfo kriging tool was used to generate an estimated surface of species distributions from a scattered set of points.

in this study indicate that the studied species were influenced by different environmental factors operating at different spatial scales. The spatial patterns of abiotic environmental variables did not fully match those of the prevalent species (Fig. 5). Thus, it is plausible that the multiple environmental variables inter- actively affect benthic macrophyte and invertebrate species (e.g. Eriksson & Bergström, 2005).

As expected, stepwise regression combining the spectra of the abiotic environment and species patterns showed that the spatial patterns of the studied macroalgal and invertebrate species were best explained by the combination of multiple environmental variables (Table 3). Spatial variability in exposure, depth, and presence of rock or gravel substrate defined the patterns of *S. arctica* and
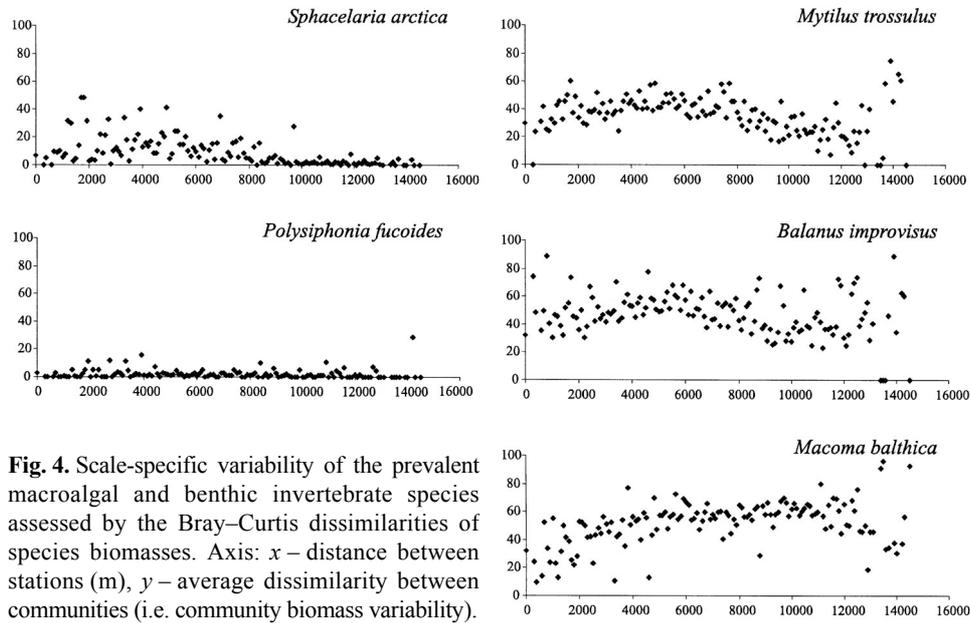
Fig. 4. Scale-specific variability of the prevalent macroalgal and benthic invertebrate species assessed by the Bray–Curtis dissimilarities of species biomasses. Axis: x – distance between stations (m), y – average dissimilarity between communities (i.e. community biomass variability).

exposure and presence of rock those of *P. fucoides*. As these macroalgae are typical hard bottom macroalgae (Martin, 1999), it is expected that the availability of suitable substrate sets the distribution limits of the species. Surprisingly, elevated spatial variability in exposure and depth significantly reduced the spatial variability of *S. arctica* on the respective scale and exposure reduced that of *P. fucoides*. Such a result is not in accordance with the previous theory that species biomasses have the highest spatial variance at the scale where environmental variability is the highest. Instead, it suggests that higher environmental patchiness at a spatial scale favours uniform patterns of macroalgae at the same scale.

It is plausible that due to poor light conditions in the study area, macroalgae cannot compete with benthic invertebrates for space (Thompson et al., 2004; Korpinen et al., 2007). High variability in exposure and/or the occurrence of flat bottoms results in an unhospitable environment of competitively superior species such as *M. trossulus* and *B. improvisus* and promotes uniform distribution pattern of the studied macroalgae. The negative effects are likely due to the higher sedimentation rate, which is known to be detrimental to the studied invertebrates (Bayne et al., 1987, 1993). In more stable exposure conditions, however, benthic invertebrates are better competitors for space and the distribution pattern of macroalgae is more stochastic and determined mainy by the patchiness of benthic invertebrates. To test the validity of this hypothesis experimenal manipulation is needed.

The presence of different sediment fractions and topographic depressions and humps resulted in stable and high biomasses of *B. improvisus*. On the other hand,
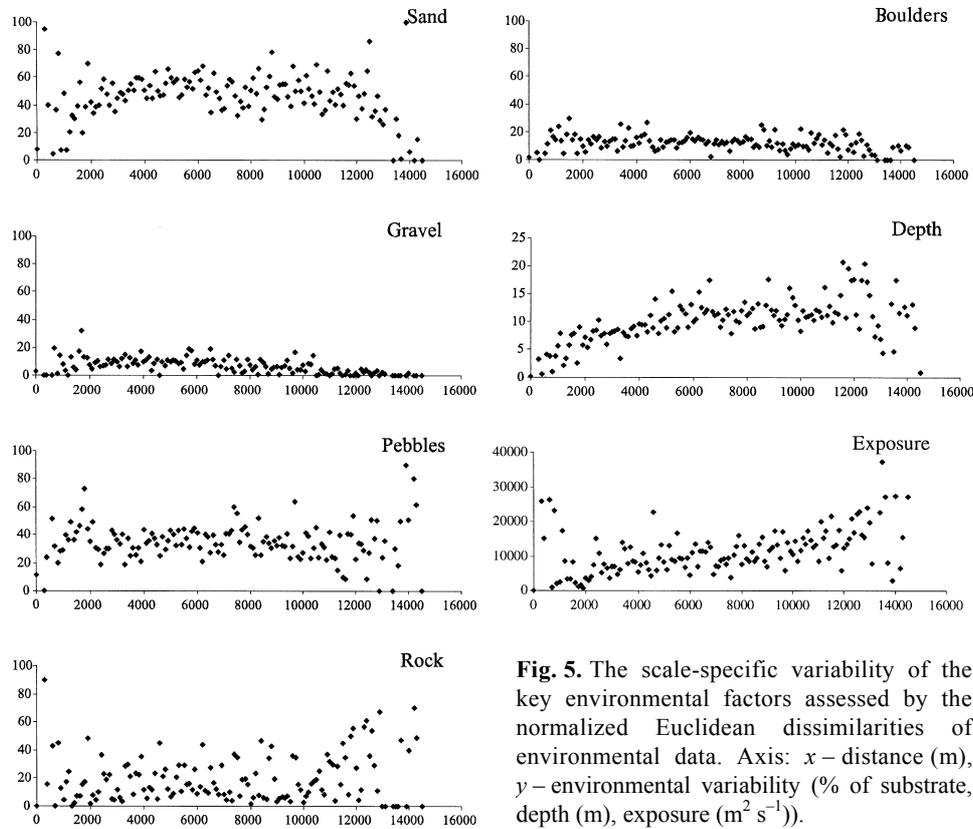
Fig. 5. The scale-specific variability of the key environmental factors assessed by the normalized Euclidean dissimilarities of environmental data. Axis: x – distance (m), y – environmental variability (% of substrate, depth (m), exposure ($m^2 s^{-1}$)).

Table 3. Results of multiple regressions of the effects of physical environmental variables on the dissimilarities of invertebrate and macroalgal species in the Gretagrund area

Model parameter	Species				
	Balanus improvisus	Macoma balthica	Mytilus trossulus	Sphacelaria arctica	Polysiphonia fucoides
R^2	0.659	0.332	0.634	0.391	0.202
p	<0.001	<0.001	<0.001	<0.001	<0.001
Depth	−0.13	0.484		−0.19	
Exposure			−0.28	−0.21	−0.21
Rock	0.585	−0.47		0.333	0.333
Boulders	0.171		0.152		
Pebbles	0.263		0.568		
Gravel	0.129			0.473	
Sand	0.409				

flat bottoms were characterized by highly variable biomasses of the species. As to *M. trossulus*, highly variable biomasses were found in more sheltered areas and higher and more uniform biomasses in more exposed areas. In addition, the distribution of *M. trossulus* was facilitated by the presence of hard bottoms.

All these results indicate that food conditions are the prime factors that regulate the distribution of *B. improvisus* and *M. trossulus* in the study area. Except for phytoplankton blooming events, the suspension feeding bivalves are often limited by the availability of suspended particulate matter (Incze et al., 1981; Fréchette et al., 1989; Smaal et al., 2001). Increasing current velocity can reduce this limitation (Walne, 1972; Fréchette & Bourget, 1985; Wildish et al., 1992). Earlier studies have shown that phytoplankton biomasses are higher in frontal areas (that are concurrent with topographic features) and in more exposed habitats (Riegman et al., 1990; Laubscher et al., 1993; Kotta et al., 2008a). It is also possible that on less exposed habitats elevated sedimentation rates are unfavourable for the settlement and growth of the species (Bayne et al., 1987, 1993).

The biomass of *M. balthica* was highly variable in areas that have patchy occurrence of hard substrate, whereas the species has less variable and high biomasses on flat bottoms. This suggests that *M. balthica* was primarily a deposit feeder in our study area and therefore confined to sedimentation habitats.

To conclude, our study demonstrated that the used methodology allows identifying the correlation scales in which environmental variability predicts the distribution of benthic communities. The study showed that the spatial variability of benthic macrophytes and invertebrates varied among species and there was no key single spatial scale where the variability of species was the highest. The study also showed that multiple environmental variables interactively affected benthic macrophyte and invertebrate species. The results of this study are useful in the further modelling of the species distributions in the northern Baltic Sea area. Likewise, the results can be applied in the planning phase of coastal monitoring, as the selected monitoring sites should capture an important fraction of total community variability. Such a task cannot be completed without prior knowledge about the spatial variability of the key organisms in the area.

ACKNOWLEDGEMENTS

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Põhjaelustiku liikide skaalaspetsiifiline levik Liivi lahes Greta madalal

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On käsitletud Liivi lahe Greta madala põhjaelustiku liikide leviku muutlikkust eri mastaapides. Greta madalal leiti 47 põhjaelustiku liiki – 11 vetikat ja 36 suurselgrootut. *Paramysis intermedia* puhul on tegemist esmaleiuga Läänemeres. Arvukamalt levisid punavetikas *Polysiphonia fucoides*, pruunvetikas *Sphacelaria arctica*, söödav rannakarp *Mytilus trossulus*, tõruvähk *Balanus improvisus* ja balti lamekarp *Macoma balthica*. On leitud statistilised seosed abiootilise keskkonna ja elustiku levikumustrite vahel. Metoodika võimaldab välja tuua olulised mastaabid, kus keskkonnatingimuste varieerumine kirjeldab kõige paremini põhjakoosluste levikut. Liikide levikumustrid eristuvad selgelt üksteisest. Keskkonnategurid eraldi ja koosmõjus kirjeldavad elustiku levikut eri mastaapides.