

Scale-specific effects of environmental variables on benthic macrophyte and invertebrate communities in the Vaindloo area, the central Gulf of Finland

Ivan Kuprijanov^{a,b}, Jonne Kotta^a✉, Merli Pärnoja^{a,b}, Kristjan Herkül^a, and Priit Kersen^a

^a Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

^b Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

✉ Corresponding author, jonne.kotta@sea.ee

Received 6 August 2010, revised 18 November 2010

Abstract. We quantified the relative importance of scale-specific variability of macroalgal and benthic invertebrate communities in the Vaindloo area, the central Gulf of Finland. Macrophyte communities had a clear variability minimum at 8 km spatial scale. In contrast to macrophytes, the scale-specific variability of benthic invertebrate communities was small with no clear variability peak or minimum. The spatial distribution patterns of macrophytes and benthic invertebrates did not vary with regard to the species composition and dominance structure of communities. Among environmental variables the coverage of boulders and depth contributed most to the variability of the species composition and biomass dominance structure of macrophytes as well as of the species composition of benthic invertebrates. In addition to these environmental factors, the variability in the abundance and biomass dominance structure of benthic invertebrates was described by coastal slope, exposure, and cover of sediment size fractions other than boulders. The study suggests that the scale-specific variability of marine communities is complex and differs notably among different ecosystem elements. The variability of macrophytes and benthic invertebrate communities was also described by the abiotic environment operating at multiple spatial scales.

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

INTRODUCTION

The majority of information on environmental conditions, biodiversity, and functioning of aquatic ecosystems has been derived from studies conducted at small spatial scales such as site or habitat scales whereas those performed at landscape or regional scales are much rarer. It has been suggested that at small spatial scales ecosystems are influenced by both abiotic forcing and biotic controls (Tilman et al., 1997; Loreau et al., 2001) while at large spatial scales abiotic forcing is considered a major force affecting the ecosystems (Steele & Henderson, 1994). However, there is no generic consensus among experts about the scale-specific effects of environmental variables on biota.

There may be situations in which the same variable has a negative, neutral, or positive effect on biota depending on the scale considered. For example, it is known that in marine ecosystems the coverage of boulder field may be inversely related to the presence of drift algae at the site scale whereas at the landscape scale it is positively related to drift algae (Kotta et al., 2008). Besides, relationships between abiotic and biotic factors that are evident at broad scales may disappear at finer scales and be replaced by the effects of biological processes (Greig-Smith, 1979; Woodward, 1987). Other studies, however, indicated a scale-independent relationship between environmental and biotic variables (e.g. Thrush et al., 2005). This points to the need for an assessment of scale-specific variability of biotic patterns and linkage of abiotic environment and associated biota.

Scaling in space and time is a central challenge in ecology. Earlier analyses suggest that variability in marine communities increases with scale (Platt & Denman, 1975); however, the theoretical expectation is inconsistent with many field observations (Hewitt & Thrush, 2009; Kotta & Möller, 2009). Some experimental studies investigating the relationship between environmental and species variability across different spatial scales found the lack of scale dependence to markedly different responses at different scales (Thrush et al., 2005). The degree of interaction between broad-scale factors with smaller scale variability varies among regions and is expected to determine the consistency of responses over large spatial scales. It is commonly thought, though, that local communities assemble from the macro- to the microscale, i.e. regional scale variability governs local variability rather than the other way round (Whittaker et al., 2001; Kotta & Witman, 2009). Nevertheless, small-scale processes can also generate large-scale patterns (Wootton, 2001). The knowledge on such species interaction, however, is poor and no generic scale-specific theories exist.

In the Baltic Sea the species diversity is low due to the low salinity and short evolutionary history of the sea (Russell, 1985; Wallentinus, 1991). Biotic interactions are commonly thought to have minor importance in controlling rocky shore (Waern, 1952; Kautsky & van der Maarel, 1990) and soft bottom communities (Herkül et al., 2006) whereas physical control is common (Kotta et al., 2004; Põllumäe & Kotta, 2007). Large-scale distribution patterns in the Baltic Sea display a high predictability related with the scale-specific effect of abiotic factors such as salinity and depth on the community structure (Kautsky, 1993; Middelboe et al., 1997; Bonsdorff & Pearson, 1999). Locally, light availability is the major environmental factor determining the species distribution of macrophytes and benthic invertebrates associated to the plants (Kautsky & van der Maarel, 1990). In addition, geological and topological conditions may affect the availability of substrates appropriate to the species present in the region (Kautsky et al., 1999). Benthic invertebrates are locally governed by the levels of primary production in shallow areas and intensity of hypoxia in deep areas (Bonsdorff & Pearson, 1999; Kotta et al., 2007). Although these studies suggest that relationship between the abiotic environment and biota is scale dependent, the spectra of environmental and biotic variability were not analysed. Therefore there is a need to resolve important scales of variability (i.e. patterns of patchiness) of macrophytes and benthic

invertebrates and to determine the linkage between the scale-specific environmental variability and biotic patterns, especially at fine scales.

In this study we quantified the relative importance of scale-specific variability of macroalgal and benthic invertebrate communities in the Vaindloo Shallow, the northern Baltic Sea. In order to establish the link between scale-specific patterns of the abiotic environment and biota, community variability was decomposed into the relative contribution of different abiotic environmental factors. We assumed that the variability in the community structure at a certain spatial scale relates to the magnitude of effects of environmental variable(s) operating at this scale. Thus, the important scales (i.e. typical patch sizes) of the key abiotic environmental variables should match the important scales of communities.

MATERIAL AND METHODS

The study was conducted in the Vaindloo Shallow, the central Gulf of Finland, the northern Baltic Sea, in June 2009 in the frame of the project “Implementation of Natura 2000 in Estonian marine areas: site selection, designation and protection measures – ESTMAR”, which is implemented by the Estonian Marine Institute and partners (Environmental Board, Estonian Ornithological Society, Estonian Fund for Nature, BEF-Estonia, BEF-Latvia, Norwegian Institute of Water Research) with the financial support of the Norwegian financial mechanisms. The overall goal of the project is to contribute to the implementation of Natura 2000 in Estonian marine areas.

The Gulf of Finland has a relatively large catchment area and abundant freshwater inflow. The surface salinity varies from 0 psu in its eastern end to 7 psu at the western areas (Pitkänen et al., 2008). Near the bottom, the salinity increases from 5 psu in the eastern parts to approximately 10 psu in the western parts. Halocline strength varies both spatially and temporally. The average seawater temperature is from 0 to 15 °C. The gulf is among the most eutrophicated basins in the Baltic Sea area (Pitkänen et al., 2007). Bottom sediments consist mainly of sand and boulders at shallower areas and silt and clay sediments rich in organic matter in deeper areas (Pitkänen et al., 2008). In our study area salinity ranged between 5 and 7 psu (Database of the Estonian Marine Institute), the average depth was 27 m and maximum 56 m. Sand, pebble, and gravel bottoms dominated.

The phytobenthos and associated benthic invertebrate sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE programme (HELCOM, 2007). A total of 114 stations were sampled and three replicate samples were taken in each station (Fig. 1). On soft bottoms sampling was performed by an Ekman type bottom grab (200 cm²; altogether 300 samples) and on hard bottoms benthic macrophytes and invertebrates were collected with a diver-operated metal frame (400 cm²; altogether 42 samples). In every station the coverage of different substrate types was estimated by a remote video-camera. The substrate classes were as follows: silt (fluffy, high in organic content <0.063 mm), clay (<0.063 mm), fine sand (0.063–0.25 mm), medium sand (0.25–0.5 mm), coarse sand (0.5–2 mm), gravel (2–20 mm), small stones with a diameter less than

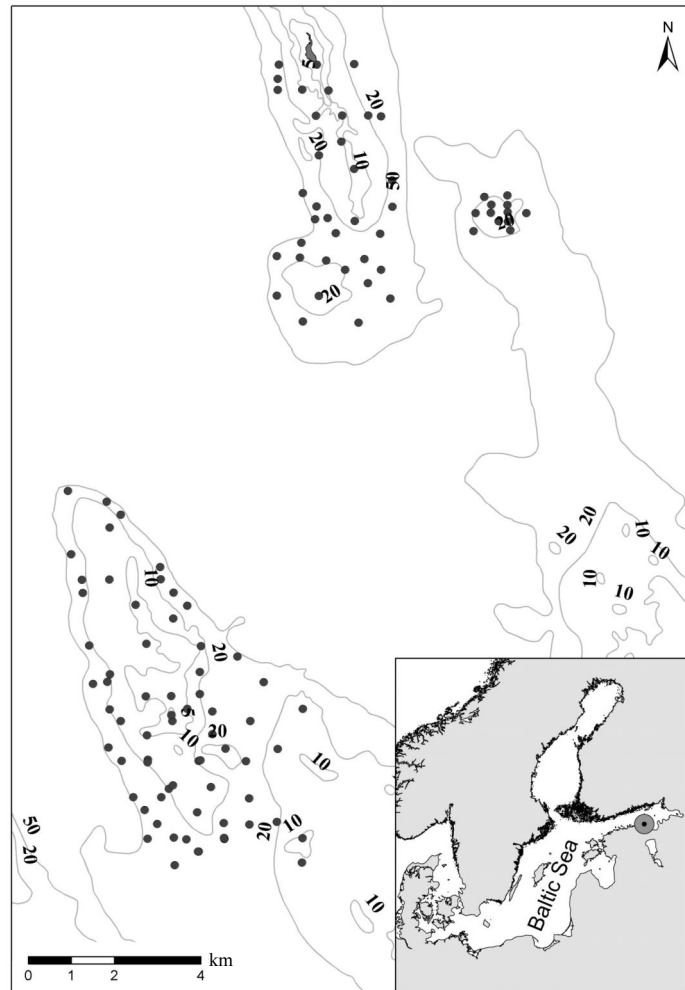


Fig. 1. Study area. The grey circle on the inset map shows the location of the Vaindloo area in the Baltic Sea. Sampling stations are indicated by small filled dots. Depth isobaths are shown by grey lines.

20 cm, boulders with diameters larger than 20 cm. The borderline between fine and medium sands could be accurately delineated with 0.25 mm mesh screens (see next paragraph); the distinction between other sediment types was made visually.

Grab and frame 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. The dry weight of each taxon was obtained after keeping the material 2 weeks at 60°C .

The 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, and the resulting

grids had a resolution of 25 m. The exposure range in the study area was calculated for 50, 100, 500, and 1000 m scales.

The inclination of coastal slopes was calculated at 50, 100, 500, and 1000 m resolutions on the basis of depth charts (available at the Estonian Marine Institute) using the Spatial Analyst tool of ArcInfo software (Anon., 2004). High values of coastal slopes indicate the occurrence of topographic depressions or humps at smaller spatial scales (50–100 m) and the occurrence of steep slopes at higher spatial scales (500–1000 m). Low values refer to flat bottoms at the measured spatial scales.

Multivariate data analyses were performed with the statistical program ‘PRIMER’ version 6.1.5 (Clarke & Gorley, 2006). Similarities between 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 ArcInfo (Anon., 2004) was used to calculate the geographical distances between the studied sites. The 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. As it is not straightforward to break down model R^2 into shares from the individual regressors, we used ‘the averaging over orderings (LMG)’ of the R package relaimpo (Grömping, 2006) in order to assess the relative importance of individual regressors to a multiple regression model (Grömping, 2007). The LMG refers to the amount of explained variance and decomposes R^2 into non-negative contributions that automatically sum to the total R^2 .

RESULTS

Macrophytes were represented by only eight species in the study area (Table 1). The most common species were the filamentous brown algae *Pilayella littoralis* and *Shpaelaria arctica* and the filamentous red alga *Ceramium tenuicorne* with 8.9%, 17.4%, and 11.6% occurrence and average biomasses of 20.0, 4.1, and 4.4 g dw m⁻², respectively. The perennial red alga *Furcellaria lumbricalis* dominated in the biomass below 10 m with an average occurrence of 3.7% and biomass of 9.1 g dw m⁻². The filamentous green alga *Cladophora glomerata* had a low biomass in the study area. The brown algae *Dictyosiphon foeniculaceus* and *Fucus vesiculosus* and the red alga *Coccolytus truncatus* were found in a single sample only and at low biomasses.

Altogether 23 benthic invertebrate species were recorded in the study area (Table 2). The deposit-feeding clam *Macoma balthica* occurred almost in every second sample and strongly dominated in the invertebrate biomass (over 50 g dw m⁻²). The clam was widely distributed reaching also the deepest sites in the study area. The suspension-feeding barnacle *Balanus improvisus* and the mussel *Mytilus trossulus* had also relatively high occurrences (30.0% and 32.6%, respectively) and biomasses (41.1 and 13.7 g dw m⁻², respectively) and were distributed over a wide range of depths. The crustacean amphipod *Monoporeia affinis* and the isopod *Saduria entomon* were observed only at deep sites of the study area with average

Scale-specific variability of benthic communities

Table 1. Average biomass \pm SE (g m^{-2}), occurrence (% of findings), and depth range (m) of macrophyte species in the Vaindloo area

Species	Biomass	Occurrence, %	Min. depth	Max. depth
Green algae				
<i>Cladophora glomerata</i> (L.) Kützing	0.11 \pm 0.05	2.6	0.7	7.0
Brown algae				
<i>Dictyosiphon foeniculaceus</i> (Huds.) Grev.	<0.01	0.5	0.7	0.7
<i>Fucus vesiculosus</i> L.	0.58 \pm <0.01	0.5		
<i>Pilayella littoralis</i> (L.) Kjellman	20.04 \pm 7.69	8.9	0.7	9.4
<i>Sphacelaria arctica</i> Harvey	4.13 \pm 0.90	17.4	6.0	15.3
Red algae				
<i>Ceramium tenuicorne</i> (Kützing) Waern	4.41 \pm 2.04	11.6	0.7	14.6
<i>Coccotylus truncatus</i> (Pallas) M. J. Wynne & J. N. Heine	0.02 \pm <0.01	0.5		
<i>Furcellaria lumbricalis</i> (Hudson) J. V. Lamouroux	9.06 \pm 6.01	3.7	8.5	10.9

Table 2. Average biomass (g m^{-2}), occurrence (% of findings), and depth range (m) of zoobenthos taxa in the Vaindloo area

Species	Biomass	Occurrence, %	Min. depth	Max. depth
Annelida				
<i>Halicryptus spinulosus</i> von Siebold	0.43 \pm 0.13	3.7	22.5	27.5
<i>Hediste diversicolor</i> (O. F. Müller)	0.18 \pm 0.07	4.7	14.6	51.0
<i>Marenzelleria neglecta</i> (Sikorski & Bick sp. nov.)	0.06 \pm 0.01	19.5	19.0	56.0
Oligochaeta	0.04 \pm 0.01	27.4	0.7	51.0
Crustacea				
<i>Balanus improvisus</i> Darwin	41.10 \pm 9.11	30.0	6.0	36.6
<i>Corophium volutator</i> Pallas	0.40 \pm 0.2	4.2	16.0	29.0
<i>Gammarus</i> juv.	0.13 \pm 0.04	20.0	0.7	17.0
<i>Gammarus oceanicus</i> Segerstråle	1.10 \pm 0.18	1.1	0.7	0.7
<i>Gammarus salinus</i> Spooner	0.16 \pm 0.05	10.0	0.7	15.0
<i>Gammarus zaddachi</i> Sexton	0.48 \pm 0.15	7.4	0.7	13.9
<i>Idotea baltica</i> Pallas	0.35 \pm <0.01	0.5	6.0	29.0
<i>Jaera albifrons</i> Leach	0.05 \pm 0.01	16.8	7.0	14.6
<i>Monoporeia affinis</i> Lindström	0.13 \pm 0.03	12.6	9.4	51.0
<i>Saduria entomon</i> L.	9.3 \pm 2.25	7.9	14.6	53.0
Miscellaneous				
Chironomidae				
<i>Electra crustulenta</i> Pallas	0.02 \pm <0.01	14.7	6.0	40.0
	<0.01	7.4	10.2	30.0
Mollusca				
<i>Cerastoderma glaucum</i> Poiret	2.15 \pm 1.03	1.6	9.4	11.8
<i>Hydrobia ulvae</i> Pennant	0.44 \pm 0.13	3.7	9.4	25.6
<i>Lymnaea peregra</i> Müller	1.47 \pm 0.45	3.7	7.0	14.6
<i>Macoma balthica</i> L.	50.40 \pm 5.02	49.5	10.2	53.0
<i>Mya arenaria</i> L.	0.15 \pm 0.01	1.1	9.4	37.0
<i>Mytilus trossulus</i> Gould	13.66 \pm 2.42	32.6	0.7	31.0
<i>Theodoxus fluviatilis</i> L.	1.02 \pm 0.18	12.6	6.0	19.0

occurrences of 12.6% and 7.9%. The deposit-feeding polychaetes *Hediste diversicolor* and *Marenzelleria neglecta* and oligochaete worms were found frequently on soft bottoms over the depth range studied at occurrences of 4.7%, 19.5%, and 27.4%, respectively. Throughout the study area no evidence of the presence of hypoxia or anoxia was observed assessed as the lack of the smell of H_2S in the samples.

Macrophyte communities had a clear variability minimum at 8 km spatial scale. In contrast to macrophytes, the scale-specific variability of benthic invertebrate communities was small with no clear variability peak or minimum. The spatial distribution patterns of macrophytes and benthic invertebrates did not vary in the species composition and dominance structure of communities (Fig. 2).

Among the abiotic variables depth, coastal slope, silt, and fine and medium fractionated sands had low scale-specific variability. Gravel coverage and exposure had a variability peak at 8 km scale whereas boulders had a variability minimum at 8 km scale. Coarse sand and small stones had a variability peak at 10 km scale (Fig. 3).

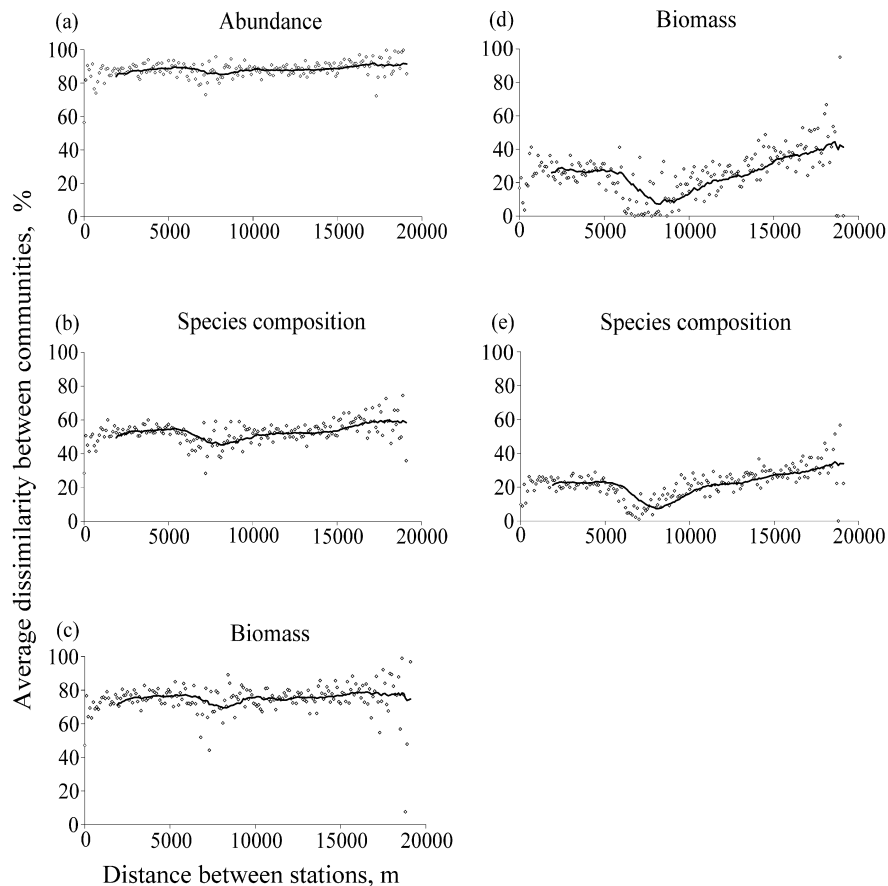


Fig. 2. Scale-specific variability of benthic invertebrate (a–c) and phytobenthic communities (d, e) assessed by the Bray–Curtis dissimilarities of species composition, abundances, and biomasses.

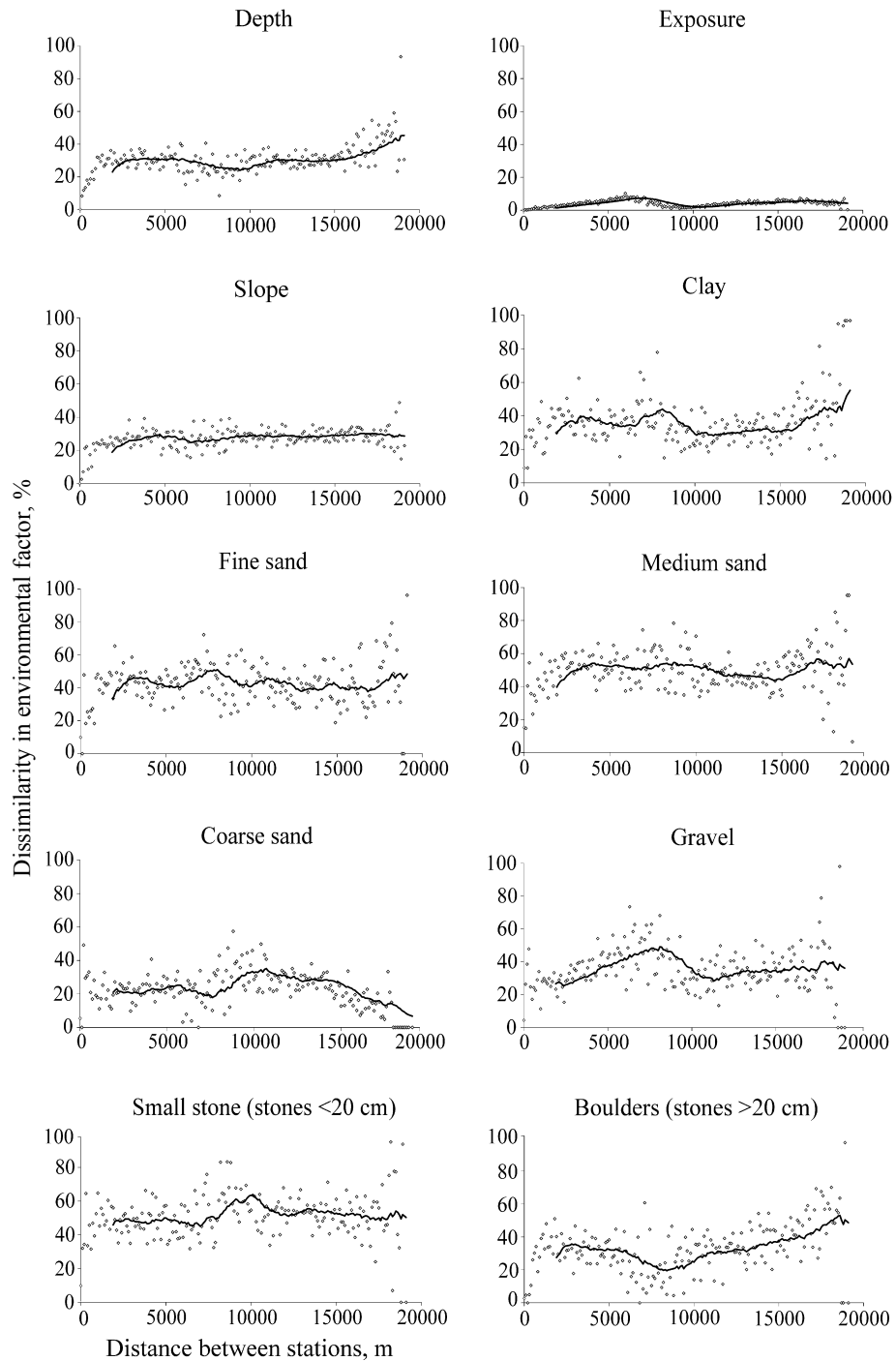


Fig. 3. Scale-specific variability of the key environmental factors assessed by the Bray–Curtis dissimilarities of environmental data. Depth was expressed in metres, exposure in $\text{m}^2 \text{s}^{-1}$, slope in degrees of grade, and substrate types in percentage cover.

Relaimpo analysis showed that the studied abiotic environmental variables significantly contributed to the distribution patterns of benthic communities (Figs 4, 5). A particularly high fit was obtained for the community composition and biomass of phytobenthos with model R^2 values estimated at 76.48% and 80.41%, respectively. Among environmental variables the coverage of boulders

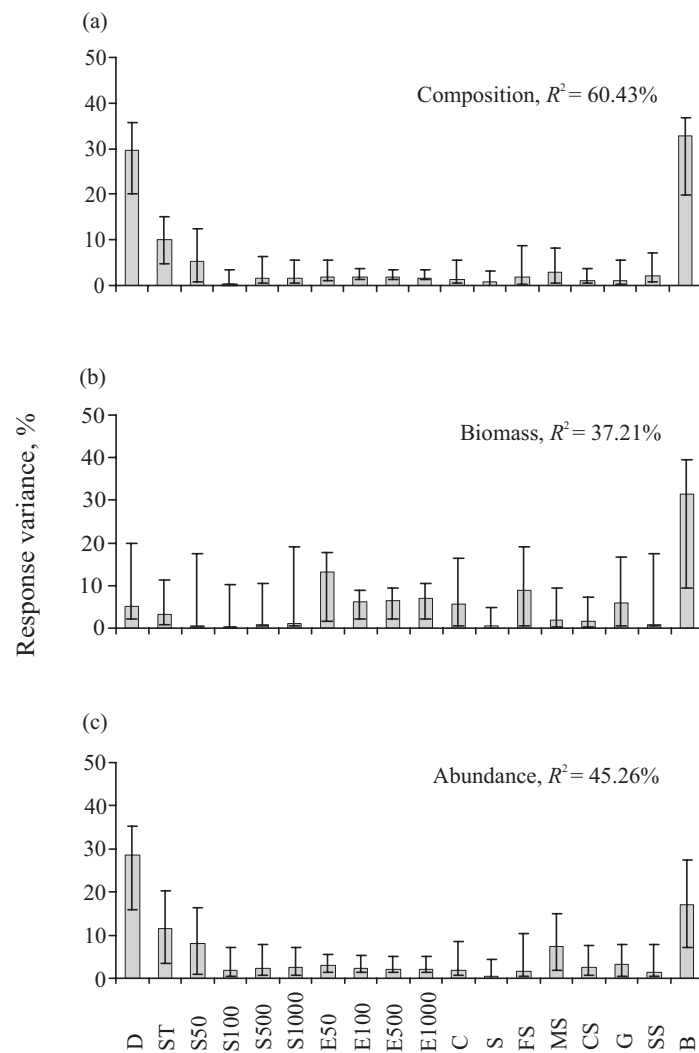


Fig. 4. Relative importance of environmental variables for benthic invertebrate communities with 95% bootstrap confidence intervals. The LMG method was used and metrics were normalized to sum to 100%. The codes of environmental variables are as follows: D – depth; ST – prevailing sediment type classified into sediment classes shown below; S50, S100, S500, S1000 – coastal slope at the respective spatial scale; E50, E100, E500, E1000 – exposure at the respective spatial scale; coverages of different sediment types: C – clay; S – silt; FS – fine sand; MS – medium sand; CS – coarse sand; G – gravel; SS – stones smaller than 20 cm; B – boulders, stones larger than 20 cm.

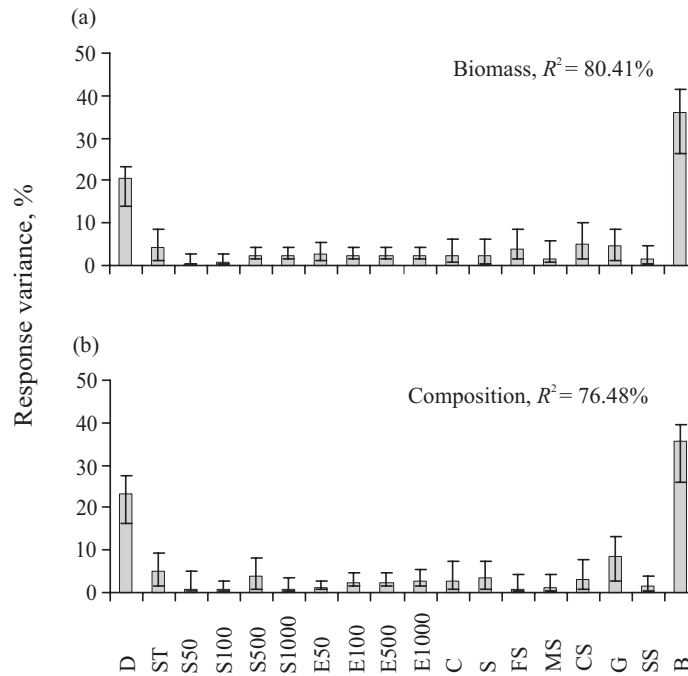


Fig. 5. Relative importance of environmental variables for macrophyte communities with 95% bootstrap confidence intervals. The LMG method was used and metrics were normalized to sum to 100%. The codes of environmental variables are as follows: D – depth; ST – prevailing sediment type classified into sediment classes shown below; S50, S100, S500, S1000 – coastal slope at the respective spatial scale; E50, E100, E500, E1000 – exposure at the respective spatial scale; coverages of different sediment types: C – clay; S – silt; FS – fine sand; MS – medium sand; CS – coarse sand; G – gravel; SS – stones smaller than 20 cm; B – boulders, stones larger than 20 cm.

and depth contributed most to the variability of species composition and biomass dominance structure of macrophytes with each variable explaining between 20% and 40% of the overall variability. Fine-scale topography (coastal slope values below 500 m scales) had a limited explanatory power in the models of phytobenthic communities with each factor explaining less than 1% of the model variability.

Similar to macrophytes, the coverage of boulders and depth largely described the variability in the species composition of benthic invertebrates with each variable explaining between 30% and 40% of the overall variability (Fig. 4). In addition to these environmental factors, the variability in the abundance and biomass dominance structure of benthic invertebrates was described by coastal slope, exposure, and cover of sediments other than boulders. Each such variable contributed up to 10% of the model variability. In contrast to benthic macrophytes, in the models of benthic invertebrate communities fine-scale topography was very important with species composition and abundance structure being explained by coastal slope values at 50 m scale and biomass structure by exposure values at 50 m scale with each explaining about 10% of the model variability.

DISCUSSION

In our study the dissimilarities of species composition, abundance, and biomass of macrophyte and benthic invertebrate species were ordered by the spatial distance between stations. Such analysis enabled to quantify the patterns of spatial variability of communities. The results suggest that the scale-specific variability of marine communities is complex and differs considerably among different ecosystem elements. Namely, the variability in the species composition and biomass of macrophytes was clearly scale-dependent whereas the patterns of species composition, abundance, and biomass of benthic invertebrates were largely scale-independent.

The studied benthic invertebrate communities were typical of the northern Baltic Sea (Bonsdorff & Pearson, 1999; Kotta et al., 2007). It is notable that sediments in the study area were very diverse and varied at multiple spatial scales reflecting the postglacial history of the region (Ignatius et al., 1981). Consequently, the coverage of different sediment types is expected to define the patterns of benthic invertebrates in the study area. Although different sediment fractions showed peaks and depressions at different scales, their cumulative effect resulted in a scale-invariant pattern of benthic invertebrates.

On the other hand, macrophyte communities in the studied area are specific in terms of species composition and dominance structure. In contrast to other sea basins the studied area is characterized by low salinity, poor water transparency, and narrow distribution of appropriate substrates resulting in low diversity and biomass of macrophytes. This is shown for example by the presence of a small number of macroalgal species and absence of higher plants. Besides, the filamentous algae such as *Cladophora glomerata*, which are causing coastal blooms elsewhere in the Baltic Sea (Golubkov et al., 2003; Kotta et al., 2008), were represented in very low biomass despite high levels of eutrophication (Pitkänen et al., 2007). Thus, due to the strong limitation of light and substrate, the distribution of macrophytes is expected to reflect primarily the patterns of depth (i.e. light) and substrate (i.e. boulders). Namely, primary production is impossible at reduced light levels and boulders offer macrophyte species necessary preconditions for their attachment (Kautsky & van der Maarel, 1990; Witman & Roy, 2009).

The studies linking abiotic environment and biotic patterns at multiple spatial scales are rare and their results are not consistent. Observations made in an estuarine fjord showed that benthic communities within a site scale (1 km) are very similar but with increasing scale (up to 100 km) the communities become dissimilar (Dethier & Schoch, 2005). As the distribution of sediments in the studied estuary was chosen to be scale-invariant, the observed pattern of benthic invertebrates was explained by scale-dependent variables such as exposure, temperature, and salinity. Exposed areas with mobile sediments are considered to be more inhospitable than sheltered areas (Gray, 2002). On the other hand, some earlier studies have suggested that local conditions are more important in the development of shallow ecosystems of the Gulf of Finland compared to processes operating at large scales (Pitkänen et al., 2001; Lehtoranta, 2003). Similarly, comparison of the effects of local (10 km), gulf (100 km), and regional scale abiotic

environment (1000 km) on the distribution of benthic invertebrates shows the strongest links at local scales (Põllumäe et al., 2009), which was plausibly due to the strong local variability in the nutrient loading and recruitment success. As shown on the eastern coast of Sweden, the links between the abiotic environment and macroalgal communities are clearly depth-dependent with exposure being more important at the shallower areas and sediment characteristics in the deeper areas (Eriksson & Bergström, 2005). Such environmental variables vary both locally and regionally and may potentially result in different patterns of macrophyte communities.

This suggests that there exists no generic scale-specific pattern of macrophytes and benthic invertebrates. Nevertheless, the search for the important scales of variability is very important when developing robust and powerful predictive models of the distribution of macrophytes and benthic invertebrates for various local management and theoretical uses. The methodology shown in our study offers a theoretical basis to decompose the effects of different abiotic environments on biota along changing spatial scales. Our study showed that the scale-dependent variability of macrophytes and benthic invertebrates was largely described by abiotic environment operating at multiple spatial scales. As such abiotic data are nowadays widely accessible (e.g. remote sensing data on bathymetry and sediment) scale-dependent patterns of species composition, abundances, and biomasses can be modelled.

ACKNOWLEDGEMENTS

Funding for this research was provided by target financed project SF0180013s08 of the Estonian Ministry of Education and Research, by the Estonian Science Foundation under grants 7813 and 8254, by a grant from the Norwegian Financial Mechanism to the project ESTMAR, and by the Central Baltic Interreg IVa Programme HISPARES.

REFERENCES

- Anon. 2004. *ArcGIS 9: Getting Started with ArcGIS*. ESRI.
- Bonsdorff, E. & Pearson, T. H. 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional-group approach. *Aust. J. Ecol.*, **24**, 312–326.
- Clarke, K. R. & Gorley, R. N. 2006. *Primer v6. User Manual/Tutorial*. Primer-E, Plymouth, UK.
- Clarke, K. R., Somerfield, P. J. & Chapman, M. G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.*, **330**, 55–80.
- Dethier, M. N. & Schoch, G. C. 2005. The consequences of scale: assessing the distribution of benthic populations in a complex estuarine fjord. *Estuar. Coast. Shelf Sci.*, **62**, 253–270.
- Eriksson, B. K. & Bergström, L. 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. *Estuar. Coast. Shelf Sci.*, **62**, 109–117.
- Golubkov, S. M., Bäck, S., Nikulina, V. N., Orlova, M. I., Anokhina, L. E. & Umnova, L. P. 2003. Effects of eutrophication and invasion of *Dreissena polymorpha* in the coastal zone of the eastern Gulf of Finland. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **52**, 218–235.

- Gray, J. S. 2002. Species richness of marine soft sediments. *Mar. Ecol. Prog. Ser.*, **244**, 285–297.
- Greig-Smith, P. 1979. Pattern in vegetation. *J. Ecol.*, **67**(3), 755–779.
- Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. *J. Stat. Softw.*, **17**, 1–27.
- Grömping, U. 2007. Estimators of relative importance in linear regression based on variance decomposition. *Am. Stat.*, **61**, 139–147.
- HELCOM. 2007. Manual for Marine Monitoring in the COMBINE Programme of HELCOM. <http://www.helcom.fi/groups/monas/CombineManual.htm> (accessed 2010-02-20).
- Herkül, K., Kotta, J., Kotta, I. & Orav-Kotta, H. 2006. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. *Oceanologia*, **48**, 267–282.
- Hewitt, J. E. & Thrush, S. F. 2009. Reconciling the influence of global climate phenomena on macrofaunal temporal dynamics at a variety of spatial scales. *Glob. Change Biol.*, **15**, 1911–1929.
- Ignatius, H., Axberg, S., Niemisto, L. & Winterhalter, B. 1981. Quaternary geology of the Baltic Sea. In *The Baltic Sea* (Voipio, A., ed.), pp. 54–103. Elsevier, Amsterdam.
- Isäus, M. 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. PhD Thesis, Department of Botany, Stockholm University, Sweden.
- Kautsky, H. 1993. Quantitative distribution of sublittoral plant and animal communities along the Baltic Sea gradient. In *Biology and Ecology of Shallow Coastal Waters* (Elftheriou, A., ed.), pp. 23–30. Olsen and Olsen, Fredensborg.
- Kautsky, H. & van der Maarel, E. 1990. Multivariate approaches to the variation in phytobenthic communities and environmental vectors in the Baltic Sea. *Mar. Ecol. Prog. Ser.*, **60**, 169–184.
- Kautsky, H., Martin, G., Mäkinen, A., Borgiel, M., Vahteri, P. & Rissanen, J. 1999. Structure of phytobenthic and associated animal communities in the Gulf of Riga. *Hydrobiologia*, **393**, 191–200.
- Kotta, J. & Möller, T. 2009. Important scales of distribution patterns of benthic species in the Gretgrund area, the central Gulf of Riga. *Estonian J. Ecol.*, **58**, 259–269.
- Kotta, J. & Witman, J. 2009. Regional-scale patterns. In *Marine Hard Bottom Communities* (Wahl, M., ed.). *Ecological Studies*, **206**, 89–99. Springer-Verlag, Berlin, Heidelberg.
- Kotta, J., Simm, M., Kotta, I., Kanošina, I., Kallaste, K. & Raid, T. 2004. Factors controlling long-term changes of the eutrophicated ecosystem of Pärnu Bay, Gulf of Riga. *Hydrobiologia*, **514**, 259–268.
- Kotta, J., Lauringson, V. & Kotta, I. 2007. Response of zoobenthic communities to changing eutrophication in the northern Baltic Sea. *Hydrobiologia*, **580**, 97–108.
- Kotta, J., Paalme, T., Püss, T., Herkül, K. & Kotta, I. 2008. Contribution of scale-dependent environmental variability on the biomass patterns of drift algae and associated invertebrates in the Gulf of Riga, northern Baltic Sea. *J. Mar. Syst.*, **74**, S116–S123.
- Lehtoranta, J. 2003. Dynamics of sediment phosphorus in the brackish Gulf of Finland. *Monogr. Boreal Environ. Res.*, **24**, 1–58.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D. A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.
- Middelboe, A. L., Sand-Jensen, K. & Brodersen, K. 1997. Patterns of macroalgal distribution in the Kattegat-Baltic region. *Phycologia*, **36**, 208–219.
- Platt, T. & Denman, K. L. 1975. Spectral analysis in ecology. *Annu. Rev. Ecol. Syst.*, **6**, 189–210.
- Pitkänen, H., Lehtoranta, J. & Räike, A. 2001. Internal nutrient fluxes counteract decreases in external load: the case of the estuarial Eastern Gulf of Finland, Baltic Sea. *Ambio*, **30**, 195–201.
- Pitkänen, H., Kiirikki, M., Savchuk, O., Räike, A., Korpinen, P. & Wulff, F. 2007. Searching efficient protection strategies for the eutrophicated Gulf of Finland: the combined use of 1D and 3D modeling in assessing long-term state scenarios with high spatial resolution. *Ambio*, **36**, 272–279.

- Pitkänen, H., Lehtoranta, J. & Peltonen, H. 2008. The Gulf of Finland. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 285–308. Springer, Berlin.
- Põllumäe, A. & Kotta, J. 2007. Factors affecting zooplankton community of the Gulf of Finland, with respect to native and introduced predatory cladoceran interactions. *Oceanologia*, **49**, 277–290.
- Põllumäe, A., Kotta, J. & Leisk, Ü. 2009. Scale-dependent effects of nutrient loads and climatic conditions on benthic and pelagic communities in the Gulf of Finland. *Mar. Ecol.*, **30**, 20–32.
- Russell, G. 1985. Recent evolutionary changes in the algae of the Baltic Sea. *J. Brit. Phycol.*, **20**, 87–104.
- Steele, J. H. & Henderson, E. W. 1994. Coupling between physical and biological scales. *Phil. Trans. R. Soc. Lond. B*, **343**, 5–9.
- Thrush, S., Hewitt, J., Herman, P. & Ysebaert, T. 2005. Multi-scale analysis of species–environment relationships. *Mar. Ecol. Prog. Ser.*, **302**, 13–26.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Waern, M. 1952. Rocky-shore algae in the Oregrund archipelago. *Acta Phytogeogr. Suec.*, **30**, 1–298.
- Wallentinus, I. 1991. The Baltic Sea gradient. In *Intertidal and Littoral Ecosystems. Ecosystems of the World*. Vol. 24 (Mathieson, A. C. & Nienhuis, P. H., eds), pp. 83–108. Elsevier, Amsterdam.
- Whittaker, R. J., Willis, K. J. & Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.*, **28**, 453–470.
- Witman, J. D. & Roy, K. 2009. *Marine Macroecology*. The University of Chicago Press, Chicago.
- Woodward, F. I. 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Wootton, J. T. 2001. Local interactions predict large-scale pattern in empirically derived cellular automata. *Nature*, **413**, 841–844.

Abiootilise keskkonna mõju põhjataimestiku ja -loomastiku koosluste ruumimuustritele Soome lahe keskosas Vaindloo madalal

Ivan Kuprijanov, Jonne Kotta, Merli Pärnoja, Kristjan Herkül
ja Priit Kersen

Uuriti makrovetikate ja põhjaloomastiku koosluste levikumustrit Soome lahe keskosas Vaindloo madalal. Makrovetikate kooslustel esines selge varieeruvuse miinimum spektri 8 km skaalaosas. Põhjaloomastiku koosluste levik oli seevastu skaalast sõltumatu. Makrovetikate liigiline koosseis, biomassi struktuur ja põhjaloomastiku liigiline koosseis seostusid kõige enam rahnude leviku ning sügavusega. Lisaks eeltoodud muutujatele kirjeldasid põhjaloomastiku arvukuse ja biomassi levikumustreid merepõhja nõlva kalle, avatus ning teiste settefraktsioonide katvus. Uuringust selgub, et põhjakoosluste levikumustrid on keerulised ja eri ökosüsteemi elementide vahel esinevad selged erinevused. Uuring näitab ka, et makrovetikate ja põhjaloomastiku koosluste levikumustreid kirjeldab peamiselt eluta keskkonna muutlikkus.