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Scale-dependent effects of nutrient loads and climatic conditions on benthic and pelagic communities in the Gulf of Finland

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Abstract

Eutrophication and climate change are ranked among the most serious threats to the stability of marine ecosystems worldwide. The effects of nutrient loads and climatic conditions vary in direction, magnitude and spatial extent. To date the factors that are behind the scale-specific spatial and temporal variability are poorly known. In this study we assessed how variability in nutrient loads and climatic conditions at local, gulf and regional scales explained the spatial patterns and temporal trends of zooplankton and benthic invertebrates in the Gulf of Finland. In general both local and gulf scale environmental variability had an important effect on benthic invertebrate species and the variability was mainly due to local nutrient loading, gulf scale temperature and salinity patterns. Zooplankton species were equally affected by environmental variability at all spatial scales, and all nutrient load and climatic condition variables contributed to the models. The combination of variables at all spatial scales did not explain the substantially larger proportion in invertebrate variability than variables at any individual scale. This suggests that large-scale pressures such as nutrient loads and change of climatic conditions may define broad patterns of distribution but within these patterns small-scale environmental variability significantly modifies the response of communities to these large-scale pressures.

Problem

Eutrophication and climate change are ranked among the major threats to the stability of marine coastal environment and can have severe impacts on near-shore biodiversity and functioning (*e.g.* McGowan *et al.* 1998; Howarth *et al.* 2000; Jackson *et al.* 2001). Nutrient loads may lead to algal blooms, accumulation of organic matter and development of anoxia, and consequently can cause significant changes in ecosystems (Andersen *et al.* 2006; Paerl 2006). The effects of climatic variability on coastal ecosystems are less known due to the mismatch of important scales between climatic conditions and biological variables. The effects of climatic conditions operate through local weather parameters such as temperature, wind, rain, snow and current patterns, as well as interactions among these (Stenseth *et al.* 2002). Shifts in climatic conditions are known to have profound ecological impacts, altering the patterns of distribution, abundance and diversity of species (Hughes 2000; Lotze *et al.* 2006). Such effects vary largely among regions, reflecting system-specific attributes and direct and indirect responses that act as a filter to modulate the responses to enrichment and climate change (Cloern 2001; Rönnberg & Bonsdorff 2004; Hewitt & Thrush 2009). As different regions respond differently to the same type of environmental stress, the areal-specific ecological responses should be described.

Taking this into account, there is no single natural scale at which the effects of nutrient loads and climatic conditions could be studied (Levin 1992; Karlson & Cornell 1998). To identify the most important governing factors one needs to determine the scales where the links between nutrient load and climatic condition variables and biotic patterns are the strongest (Steele & Henderson 1994). Although it is recognized that processes affect ecosystems simultaneously at many spatial scales (Steele & Henderson 1994; Denny *et al.* 2004), to date the relative importance of small- and large-scale processes in the formation of marine communities is little known (*e.g.* Hewitt *et al.* 2007). Large-scale environmental stresses and disturbances (*e.g.* climatically driven changes in seawater temperature, sea level or the intensity of ice scouring) can synchronize population changes over wide geographical areas and define broad patterns of distribution, if they have a direct effect on recruitment or mortality. Within these patterns, smaller-scale processes operate at a lower intensity to modify distributions, abundances and functioning of communities (Kotta & Witman 2009). Recently, it was shown that the degree of interaction between large-scale environmental factors and smaller scale variability was not consistent across sites or species. Knowledge about such variability may affect our ability to predict effects of nutrient loads and changing climatic conditions on coastal communities (Hewitt & Thrush 2009).

In this study we evaluated how nutrient load and climatic condition variables estimated at local (10s km), gulf (100s km) and regional scales (1000s km) contributed to the biomass of zooplankton and benthic invertebrate species in a shallow brackish water ecosystem of the Baltic Sea. Nutrient loads have been an increasing ecological threat in the Baltic Sea for the past 50 years. During this time the load of nutrients has grown fourfold for nitrogen and eight times for phosphorus, leading to an increased production at all trophic levels in the ecosystem (Elmgren 2001; Rönnberg & Bonsdorff 2004). Although rising temperature has caused major shifts in the community structure in many European water bodies (*e.g.* Conners *et al.* 2002), such temperature-induced shifts have not been observed in the Baltic Sea in recent decades. It is plausible that recent changes in the mean water temperature are not ecologically important as large seasonal variation counteracts the potential effects of recent global warming. On the other hand, the indirect effects of global warming can be important and can potentially affect the structure and function of the Baltic coastal communities.

Mesozooplankton is both passively and actively mobile and capable of moving both vertically and horizontally in the aquatic environment. Their mobility allows them to transfer materials between different environments and to give mesozooplankton the potential to form strong links between different subsystems (Lundberg & Moberg 2003). Therefore it is expected that the biomasses of mesozooplankton are influenced by large-scale environmental variability rather than small-scale environmental variability. Benthic invertebrates, however, are thought to be relatively stationary, longer lived and temporally less variable than mesozooplankton. However, benthic invertebrates do not behave as a single entity and there exists a large within-group variability among benthic invertebrates. Earlier studies have shown that suspension-feeders are directly linked to pelagic primary productivity (Cloern 1982; Kotta & Møhlenberg 2002) and benthic grazers and deposit-feeders to benthic primary productivity (Granéli & Sundbäck 1985; Orav-Kotta & Kotta 2004; Kotta *et al.* 2006). Thus, it is expected that local variables explain better the distribution of benthic grazers and deposit-feeders and large-scale variables that of benthic suspension-feeders. Besides, mobile benthic species possess the ability to escape direct small-scale physical disturbances or food depletion, whereas non-migrating benthic species are more susceptible to such disturbances and rely completely on local food levels (*e.g.* Tillin *et al.* 2006; Kotta *et al.* 2008). Therefore it is also expected that local variables explain better the distribution of non-migrating benthic species and large-scale variables that of mobile benthic species.

Study Area

The study was conducted in the Gulf of Finland, Northern Baltic Sea. The average depth of Gulf is 37 m and the maximum depth 123 m. Sand, silt or sandy clay bottoms dominate. The Eastern Gulf of Finland receives fresh water from a huge drainage area and the Western Gulf is a direct continuation of the Baltic Sea proper, therefore the gulf has a permanent east–west gradient of salinity. The salinity range of stations was 2.2–7.3 psu. The area is influenced by diffuse and point source nutrient loads.

The Water Framework Directive 2000/60/EC (WFD) is the most significant piece of European water legislation that prevents further eutrophication of the ecosystem of the Gulf of Finland. According to the directive the waters of the Gulf of Finland have been divided into water bodies and the assessment of the ecosystem state is made by these basic management units. In our study we evaluated relationships between nutrient loads, climatic conditions and ecosystem variables by each water body to provide a better ecological basis for the WFD classification scheme.

Material and Methods

Within each water body two stations were sampled between 1996 and 2005 (Fig. 1, Table 1). Zoobenthos samples were collected each year during May using a Van Veen grab (0.1 m^2). The depth of sampling sites ranged from 8 to 100 m and encompassed coarse sand, medium sand and silt sediments. Grab samples were sieved in the field on 0.25-mm mesh screens. The residues were stored at −20 °C and subsequent sorting, counting and determination of invertebrate species were performed in the laboratory using a stereomicroscope. All species were determined to the species level except for oligochaetes and insect larvae. The dry weight of species was obtained after drying the individuals at 60 °C for 2 weeks. During sampling we recorded near-bottom oxygen (minimum layer) and depth-integrated salinity values.

Zooplankton was collected at the same stations as used for zoobenthos samples in May and August over 1996–2005. The samples were collected by vertical tows with a Juday closing plankton net (mesh size 90 μm, mouth area 0.1 m^2). The samples were preserved in 4% formaldehyde solution in seawater. The abundances of zooplankton species were estimated from a number of subsamples according to the methods recommended by HELCOM (1988). Biomasses (wet weights) were calculated using the

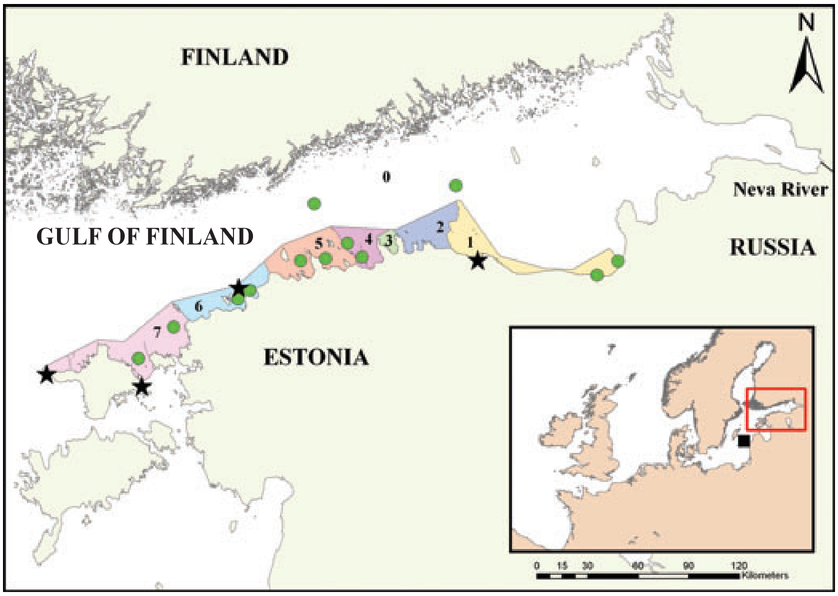

Fig. 1. Sampling locations (circles), weather stations (asterisks) and water bodies along the Estonian coastline in the Gulf of Finland. Water bodies 1–7 are defined by the EU Water Framework Directive, water body 0 represents the offshore conditions of the Gulf of Finland. Black square on minimap indicates the location of Gotland Basin.

Table 1. Characteristics of the studied water bodies (WB0…7) in the Gulf of Finland.

Environmental characteristics	WB0	WB1	WB4	WB5	WB6	WB7
Water renewal time, years	1.1	1.4	0.8	0.4	0.3	0.1
Average depth, m	65	21	52	37	27	13
Mean water flow from rivers, $m^3 \cdot s^{-1}$	0.0	>400	<5	10…20	10…20	<1
Near-bottom oxygen concentration, $ml \cdot l^{-1}$	4.6	7.7	5.2	8.4	8.7	8.1
Salinity	6.3	4.5	6.4	6.2	6.2	6.3
Sea surface temperature in May	5.9	8.8	6.7	5.8	7.8	9.1
Air temperature in May	9.0	9.5	8.9	9.1	9.1	8.5
Wind speed in May	3.5	3.5	3.5	3.4	3.4	3.1
Nitrogen load from point sources into a water body, $t \cdot year^{-1}$	0.0	434.1	0.1	827.2	6.0	0.0
Phosphorus load from point sources into a water body, $t \cdot year^{-1}$	0.0	8.9	0.0	57.4	1.2	0.0
Riverine nitrogen load into a water body, $t \cdot year^{-1}$	0.0	8941.7	115.0	1739.2	1487.1	0.0
Riverine phosphorus load into a waterbody, $t \cdot year^{-1}$	0.0	798.4	4.4	32.3	31.7	0.0

biomass factors for different taxonomic groups and developmental stages (Hernroth 1985).

The data on the annual point source and riverine loads of total N and total P to the Gulf of Finland in 1996–2005 was obtained from the Estonian Ministry of Environment and from the MARE homepage (http://www.mare.su.se/). The data of annual total N and total P loads and runoff of River Neva was obtained through Baltic-Nest (http://nest.su.se/nest/) from NW Administration of Roshydromet (Russia). The loads into six water bodies of the Estonian coast of the Gulf of Finland were used as nutrient load variables at the local scale. In general, the diffuse nutrient loads were the major type of loading in the study area. Depending on the water body the contribution of the diffuse nutrient N loads to the total N loads varied between 68 and 100% and the contribution of the diffuse nutrient P loads to the total P loads between 35 and 100%. The sum of loads due to Estonia, Finland and Russia represented nutrient load variables at the gulf scale. The concentrations of total N and total P in the Central Baltic Sea in winter were used as a proxy of regional nutrient load variables because the plankton has not yet taken up the nutrients. Inorganic nutrients that have accumulated during the winter are assimilated during the following spring bloom (HELCOM 2002).

As a proxy of atmospheric conditions the winter index of the North Atlantic Oscillation was used to relate the global climate pattern to the variation of biological data in the study area (NAO December–March, http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter. html) (Barnston & Livezey 1987; Ottersen *et al.* 2001). The NAO is an alternation in the pressure difference between the subtropical atmosphere high-pressure zone centred over the Azores and the atmospheric low-pressure zone over Iceland. NAO's connection with the wind, temperature and precipitation fields is strongest during winter. The link between the NAO and sea water temperature may persist over the summer, however, being highly region-dependent and should be assessed for each site separately (*e.g.* Ottersen *et al.* 2001). During the years of high NAO there is a substantial increase in the rainfall and consequently of the fresh-water inflow into the Baltic Sea (Hänninen *et al.* 2000). The increased pressure differences result in higher winter temperatures in Northern Europe (Rogers 1984). As an additional global climatic conditions variable, we used the Baltic Sea Index (BSI), which is the difference of normalized sea level pressures between Oslo in Norway and Szczecin in Poland. The BSI is significantly related to NAO and is used as a regional calibration of the North Atlantic Oscillation index (Lehmann *et al.* 2002). As the local, gulf and regional scale proxies of climatic condition variables we used average wind speed, air and water temperatures, water column salinity and near-bottom oxygen concentration and water temperatures at the respective scale obtained from the Estonian Hydrometeorological Institute (Table 2).

Multivariate data analyses on abiotic environment and invertebrate communities were performed by the statistical program PRIMER version 6.1.5 (Clarke & Gorley 2006). Invertebrate biomass data were square-root transformed to down-weigh the dominant species and increase the contribution of rarer species in the multivariate analysis. Similarities between each pair 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). Environmental variables were normalized prior to analyses. Non-metric multidimensional scaling analysis (MDS) on square-root transformed data of macrobenthic biomasses was used to quantify the dissimilarities between study areas and invertebrate species. Statistical differences in benthic invertebrate and mesozooplankton communities among water bodies were assessed by the ANOSIM permutation test (Clarke 1993).

BEST analysis (BVSTEP procedure) was used to relate the patterns of environmental variables measured at local, gulf and regional scales to the biomasses of invertebrate species. The analysis shows which environmental variables best predict the observed biotic patterns. A Spearman rank correlation (r) was computed between the similarity matrices of environmental data (abiotic variables; Euclidean distance) and different invertebrate species (a zero-adjusted Bray–Curtis distance). A global BEST match permutation test was run to examine the statistical significance of observed relationships between environmental variables and biotic patterns. The separate and additive contribution of nutrient loads and climatic condition variables was assessed in one analysis and the contribution of local, gulf and regional scale variables in another analysis.

Results

Generally, correlations between the studied abiotic environmental variables were poor ($P > 0.05$). Among nutrient load variables there were significant correlations between total N at 10 m surface layer in Gotland Basin during winter and total P at 10 m surface layer in Gotland Basin during winter (Spearman rank correlation, $R = 0.47$, $P < 0.05$), total N and total P point discharges at local scale ($R = 0.98$, $P < 0.001$), total N point discharge and riverine total P load at local scale ($R = 0.85$, $P < 0.001$) and among climatic condition variables between sea surface temperature predicted by nearest air temperature and sea surface temperature at station during

Table 2. The list of the studied abiotic variables with their relation to spatial scale, nutrient loads and climatic conditions.

Variable	Nutrient loads	Climatic conditions	Regional	Gulf	Local
Total N at 10 m surface layer in Gotland Basin during winter	+		+		
Total P at 10 m surface layer in Gotland Basin during winter*	+		+		
Total N at 220 m in Gotland Basin	+		+		
Total P at 220 m in Gotland Basin	+		+		
Nearbottom oxygen concentration in Gotland Basin	+		+		
Total Finnish N load into GoF	+			+	
Total Finnish P load into GoF	+			+	
Average near-bottom oxygen concentration in GoF	+			+	
Total Estonian N load into GoF*	+			+	
Total Estonian P load into GoF	+			+	
Near-bottom oxygen concentration at station during sampling	+				+
Total riverine N load into a water body	+				+
Total riverine P load into a water body	+				+
Total N load from point sources into a water body	+				+
Total P load from point sources into a water body*	+				+
NAO_{decmar}		+	+		
BSI		+	+		
Maximum ice cover in the whole Baltic Sea during winter		+	+		
Salinity at 100 in Gotland Basin		+	+		
Sea surface temperature in Gotland Basin in May		+	+		
Average number of days with wind >5 $m \cdot s^{-1}$ in all weather stations		+		+	
Average salinity in GoF		+		+	
Average air temperature during May–August in all weather stations		+		+	
Average wind speed during May in all weather stations*		+		+	
Average salinity at station during sampling		+			+
Sea surface temperature at station during sampling		+			+
Average yearly air temperature at nearest weather station		+			+
Average yearly wind speed at nearest weather station		+			+
Sea surface temperature predicted by nearest air temperature*		+			+
Number of days with wind >5 $m \cdot s^{-1}$ at nearest weather station*		+			+
Average air temperature during May at nearest weather station*		+			+
Average wind speed during May at nearest weather station*		+			+

An asterisk denotes variables not used in the statistical analyses.

sampling ($R = 0.52$, $P < 0.05$), sea surface temperature predicted by nearest air temperature and average air temperature during May at nearest weather station ($R = 0.64$, $P < 0.05$) and average yearly wind speed at nearest weather station and average wind speed during May at the nearest weather station ($R = -0.53$, $P < 0.05$). Therefore, total P at 10 m surface layer in Gotland Basin during winter, total Estonian N load into the Gulf of Finland, total P load from point sources into a water body, average wind speed during May in all weather stations, sea surface temperature predicted by nearest air temperature, number of days with wind >5 m·s^{-1} at nearest weather station, average air temperature during May at nearest weather station and average wind speed during May at nearest weather station were excluded from the further statistical analysis. The lack of other strong correlations suggested that colinearity was never a problem for the final models.

Altogether, 27 benthic invertebrate and 21 zooplankton taxa were identified in the study area. *Macoma balthica*, *Monoporeia affinis*, *Saduria entomon*, *Acartia* spp., *Eurytemora affinis* and *Synchaeta baltica* were the most fre-

Table 3. Average biomass of benthic (mg·dry weight·m^{-2}) and pelagic (mg·wet weight·m^{-2}) in each water body in May 1996–2005.

Species/taxon	WB 0	WB 1	WB 4	WB 5	WB 6	WB 7
Benthic invertebrates						
Balanus improvisus	0	0	0	0	2	89
Bylgides sarsi	0	0	0	6	0	0
Cerastoderma glaucum	0	0	0	0	0	1584
Chironomidae larvae	0	0	0	0	192	8
Corophium volutator	0	2	0	5	0	118
Gammarus salinus	28	0	0	0	0	15
Halicryptus spinulosus	0	0	59	111	30	16
Hediste diversicolor	0	0	0	0	0	48
Hydrobia ulvae	0	0	0	3	4	23
Hydrobia ventrosa	0	0	0	5	2	0
Idotea chelipes	0	0	0	0	0	0
Jaera albifrons	0	0	0	0	0	0
Macoma balthica	497	16,970	10,127	33,513	35,495	21,491
Manayunkia aestuarina	0	0	0	0	0	0
Monoporeia affinis	48	107	17	94	2	6
Mya arenaria	0	0	0	127	57	10,370
Oligochaeta	0	13	0	0	2	9
Pontoporeia femorata	184	0	5	0	1	0
Potamopyrgus antipodarum	0	6	0	0	26	0
Pygospio elegans	0	0	0	0	0	0
Saduria entomon	887	629	112	501	0	29
Theodoxus fluviatilis	0	18	0	0	0	59
Trichoptera larvae	0	0	0	0	0	1
Total zoobentos	1673	17,745	10,319	34,373	35,818	33,889
Pelagic invertebrates						
Acartia spp.	879	23	361	349	177	211
Balanus improvisus nauplii	0	0	0	0	0	2
Bivalvia larvae	77	976	689	269	15	46
Bosmina maritima	4	15	0	2	1	0
Centropages hamatus	32	0	29	8	2	10
Cercopagis pengoi	0	0	0	0	0	0
Cyclopidae	10	32	2	1	0	0
Eurytemora affinis	699	66	224	43	34	56
Evadne nordmanni	34	13	8	21	24	28
Frittillaria borealis	179	4	185	185	169	69
Keratella cochlearis	0	1	0	0	0	0
Keratella cruciformis	0	0	0	0	0	0
Keratella quadrata	20	19	5	3	0	1
Limnocalanus macrurus	587	106	336	6	6	1
Pleopsis polyphemoides	0	0	0	1	0	15
Podon intermedius	0	0	0	0	1	0
Pseudocalanus elongatus	156	1	310	14	7	13
Synchaeta curvata	0	0	0	0	2	21
Synchaeta monopus	20	2	5	4	43	4
Synchaeta baltica	1992	167	1097	1936	512	407
Temora longicornis	30	1	39	14	4	11
Total zooplankton	6731	1594	4392	4793	1554	1329

quently detected taxa. The total biomass of benthic and pelagic invertebrates in samples ranged from 0 to 188 g·dry weight·m^{-2} and from 3 to 62,000 mg·wet weight·m^{-2}, respectively (Table 3).

When all biomasses of pelagic and benthic invertebrates were pooled, the ordination of stations reflected the east–west gradients of the Gulf of Finland. ANOSIM analysis confirmed the trend and showed that most water bodies were significantly different in terms of the biomass structure, *i.e.* the studied water bodies behave independently of each other (global R = 0.448, $P < 0.001$) (Fig. 2).

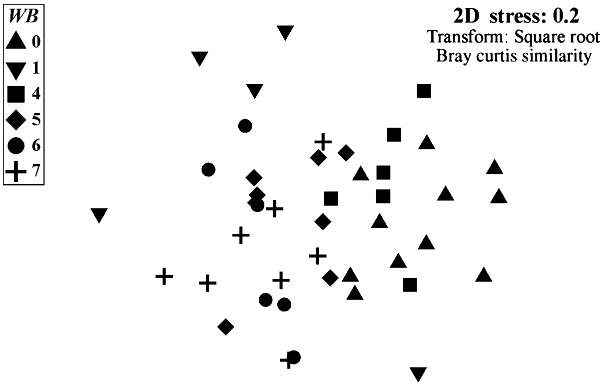

Fig. 2. Similarity of water bodies according to the benthic and pelagic invertebrate communities. Pooled samples collected within each water body and each year during the late spring (May) were used for this ordination.

Pelagic species had larger spatial and temporal variability of biomasses compared to that of benthic invertebrate species. In terms of spatial and temporal variability patterns the majority of benthic invertebrate species were statistically distinguished from zooplankton species (ANOSIM test, $P < 0.05$). However, mobile benthic species such as *Corophium volutator*, *Pontoporeia femorata*, *M. affinis* and *S. entomon* were statistically dissimilar from zooplankton species (ANOSIM test, $P > 0.05$). Small and abundant rotifers were placed inside the zooplankton cluster but close to the non-migrating benthic species, whereas larger and less dominating copepods were separated from the non-migrating benthic species (Fig. 3).

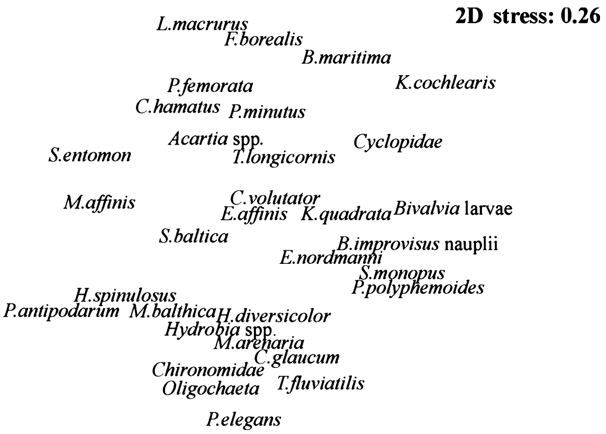

Fig. 3. Ordination of taxonomic groups; pooled samples collected within each water body and each year during the late spring (May) were used.

The relationship between abiotic environment and benthic invertebrate species was strongest at local and gulf scales (depending on the species, Spearman rank correlations varied between r = 0.19 and 0.38) and weak at regional scale (r = 0–0.17). The regional scale variability was significant only for *Halicryptus spinulosus* (r = 0.11), *Mya arenaria* (r = 0.14) and *M. balthica* (r = 0.18). The combination of variables at all spatial scales did not explain the substantially larger proportion of benthic invertebrate variability than variables at any individual scale (difference in $r_{\text{all scales combined}-\text{any scale}} = 0$–$0.05$) (Fig. 4).

In contrast to benthic invertebrates the relationship between abiotic environment and zooplankton species was often described by abiotic variability at all spatial scales studied (depending on the species Spearman rank correlations varied between r = 0.18 and 0.42). As an exception, the biomass of bivalve larvae and *Pleopsis polyphemoides* in May was only described by environmental variability at local scale (r = 0.18 and r = 0.19) (Fig. 5).

Among benthic invertebrates *P. femorata, H. spinulosus*, *Hydrobia* spp., Oligochaeta and Chironomidae larvae were described only by nutrient load variables (r = 0.18–0.56) and *S. entomon* and *Hediste diversicolor* only by climatic condition variables (r = 0.17–0.37). Among mesozooplankton, *P. polyphemoides* and bivalve larvae were described only by nutrient load variables (r = 0.17–0.18) and *Bosmina maritima* and *Keratella quadrata* by climatic condition variables in May (r = 0.23–0.27). *Pleopsis polyphemoides* was explained by nutrient load variables (r = 0.56) and *S. baltica* and Cyclopidae by climatic condition variables in August, respectively (r = 0.33–0.37). All other benthic and zooplankton species were related to both climatic conditions and nutrient load variables (r = 0.17–0.63) (Fig. 6). In the biomass models of zooplankton species the contribution of nutrient load variables increased almost linearly with the contribution of climatic condition variables (Fig. 7). For some dominant benthic invertebrate species such as *M. affinis*, *Potamopyrgus antipodarum* and *Theodoxus fluviatilis* the links between environmental variability and biotic patterns were not statistically significant. For mesozooplankton the models for *Balanus improvisus* larvae, Cyclopidae and *Cercopagis pengoi* were not statistically significant in May

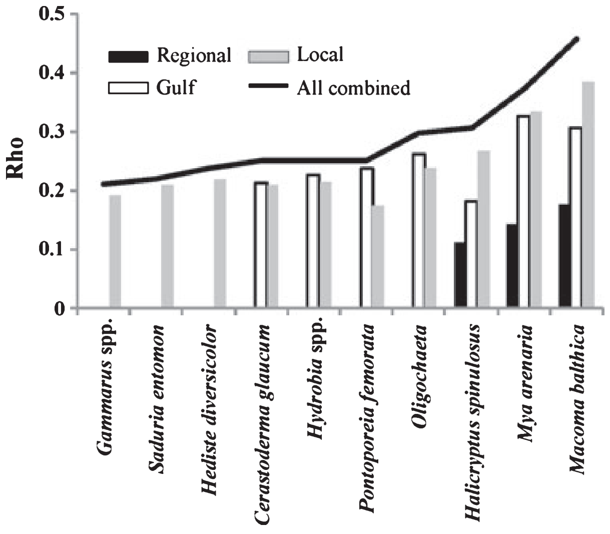

Fig. 4. Separate and combined effects (Rho, BVSTEP) of abiotic environmental variables at different spatial scales on benthic invertebrate species. Only significant relationships are shown.

and the models for *Balanus improvisus* larvae, *Limnocalanus macrurus* were not significant in August.

Discussion

The main findings of the study are that (i) the effect of local and gulf scale environmental variability was important on benthic invertebrate communities and (ii) the variability was mainly due to local nutrient loading, gulf scale temperature and salinity patterns. In addition, we found that (iii) zooplankton species were equally affected by environmental variability at all spatial scales and that (iv) all nutrient loads and climatic condition variables contributed to the models of zooplankton species.

This suggests that large-scale pressures such as nutrient loads and change of climatic conditions may define broad patterns of distribution but that within these patterns, small-scale environmental variability significantly modifies the response of communities to these large-scale pressures. As such, this confirms the recent findings of Hewitt & Thrush (2009) on the nature of scale-dependent interactions between climatic condition variables and benthic invertebrate patterns, supports the multiscale theory that assumes interactions between processes operating over different scales (*e.g.* Wu *et al.* 2000), and can be used to predict location-dependent responses of the studied broad-scale factor in the Gulf of Finland. Our study also suggests that the consistency of effects of broad-scale factors likely depends on the degree of the small-scale heterogeneity of habitat (models included those local variables that are known to have large variability) and the developmental characteristics of species (pelagic *versus* benthic species, larval development *versus* direct development) (Kotta & Witman 2009). Our results show a clear difference between how benthic invertebrates and mesozooplankton responded to changes in nutrient load and climatic condition variables. Namely, the predictive power of the benthic invertebrate model was highest using a mixture of local and gulf scale variables. In contrast, for the mesozooplantkton model, all studies scales were statistically significant.

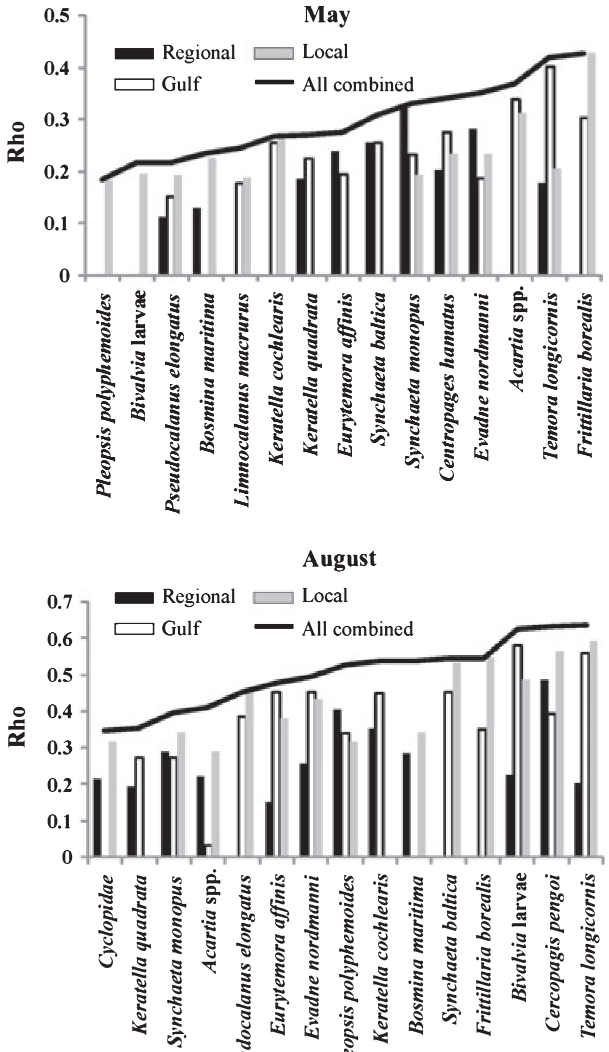

Fig. 5. Separate and combined effects (Rho, BVSTEP) of abiotic environmental variables at different spatial scales on zooplankton species. Only significant relationships are shown.

Increasing nutrient loads are known to lead to higher abundances and biomasses of benthic invertebrates, but too high concentrations are known to cause hypoxia and disappearance of the species (Posey *et al.* 1999; Kotta

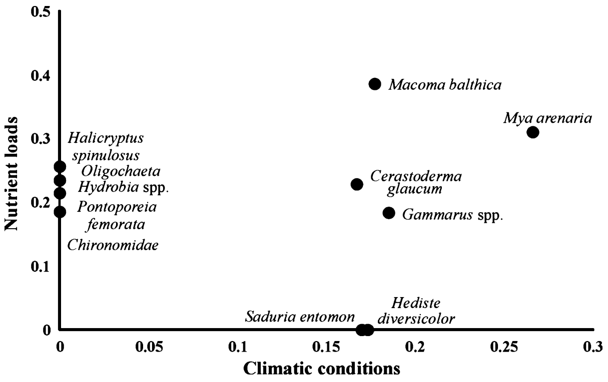

Fig. 6. Relationship (Rho, BVSTEP) between nutrient loads, climatic condition variables and benthic invertebrate species. Only significant relationships are shown.

et al. 2000, 2007; Karlson *et al.* 2002). Among benthic invertebrates, *Pontoporeia femorata*, Oligochaeta, *Hydrobia* spp., *Halicryptus spinulosus*, and Chironomidae larvae were only related to nutrient load variables. The former two species are severely decimated at low oxygen levels and the strong inverse relationship between nutrient load variables and invertebrates may refer to the negative consequences of hypoxia to the named species. On the other hand, *Hydrobia* spp. prefer elevated nutrient loads and tolerate moderate hypoxia. The latter two taxa are the typical inhabitants of severe organic enrichment and hypoxic conditions and the positive relationship between nutrient load variables and biomasses indicates the facilitative effect of nutrient loading on the species (Kotta & Orav 2001; Lauringson & Kotta 2006).

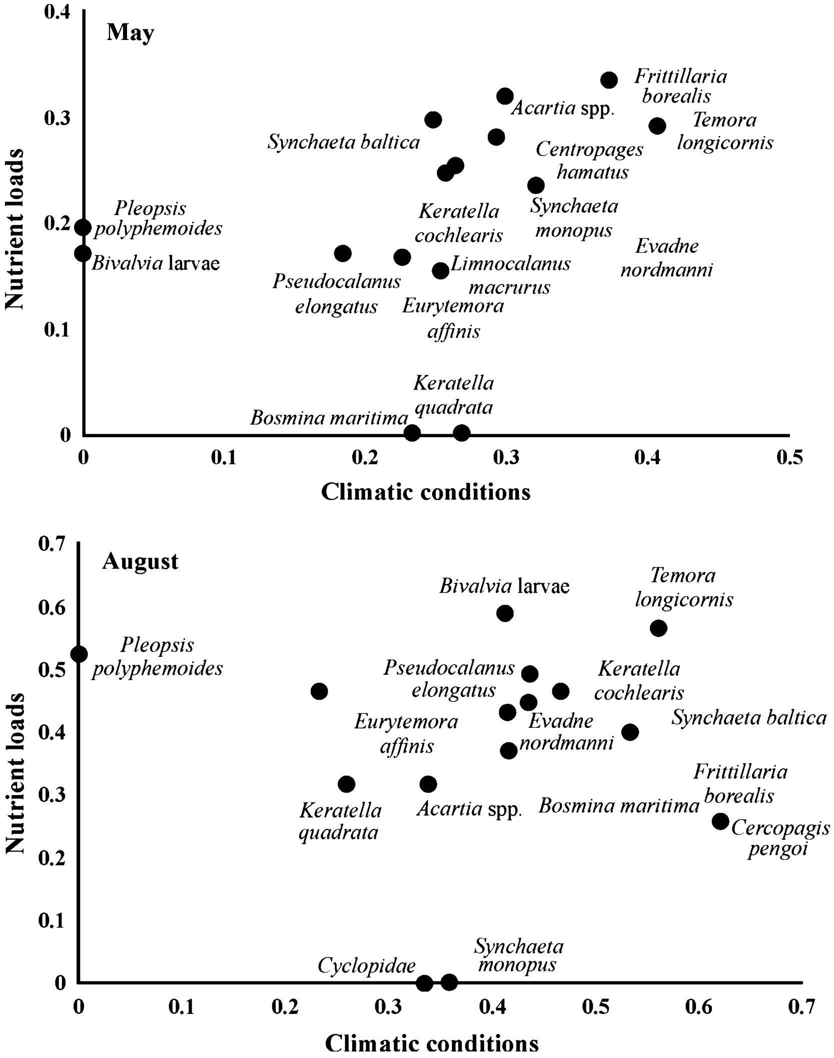

Fig. 7. Relationship (Rho, BVSTEP) between nutrient loads, climatic condition variables and zooplankton species. Only significant relationships are shown.

We are not aware of any studies reporting clear evidence of the links between nutrient load variables and zooplankton communities in the Baltic and North Sea areas (*e.g.* Colijn *et al.* 2002). There is some indication that the density of adult *Temora longicornis* increases with eutrophication level (Fransz *et al.* 1992). Besides, nutrient loading is known to correlate with mesozooplankton communities in the Gulf of Finland (Põllumäe & Kotta 2007). However, the latter study did not take into account other abiotic factors (*e.g.* weather patterns, long-term hydrology) that may be behind this relationship. In fresh-water ecosystems, nutrient loading is known to raise the biomass and change the species composition of zooplankton (Ostoji 2000; Kangur *et al.* 2002; Straile & Geller 1998). In this respect our result on the significant interactions between nutrient load variables and zooplankton communities in the brackish Gulf of Finland should be treated as exceptional. Our study not only reports zooplankton total biomass but also takes into account the community composition. Total biomass, as solely reported in many other studies, may not capture the links between nutrient load variables and the responses of separate zooplankton species.

Change of climatic conditions is known to cause the massive blooms of benthic invertebrates (Lawrence 1975), replacement of key species (Southward *et al.* 1995) and other major shifts in community structure (Conners *et al.* 2002). Among other effects benthic communities are exposed to severe winter storms and reduced ice scour under rapidly changing climate (Gutt 2001; Strasser *et al.* 2001). We are not aware of studies reporting the effects of climatic conditions on the distribution of benthic species in the Baltic Sea.

In our study the distribution of *Saduria entomon* and *Hediste diversicolor* was only related to climatic condition variables. Similarly, the distribution of *Macoma balthica*, *Cerastoderma glaucum*, *Mya arenaria* and *Gammarus salinus* also had a large component of climatic condition variability. In contrast, the distribution of these species was previously thought to be largely regulated by trophic status of the Baltic Sea (*e.g.* Kotta *et al.* 2007). At the same time the population dynamics of the bivalves is strongly related to seawater temperatures in Northwestern European estuaries where a series of mild winters results in low bivalve recruit densities and small adult stocks (Philippart *et al.* 2003). In the North Sea area, however, low temperatures strongly affect *Cerastoderma edule* but cause no increased mortality in *M. arenaria* or *M. balthica* (Strasser *et al.* 2001). It is likely that changes in the mean water temperature of the Baltic Sea are not very important for benthic invertebrates as large seasonal variation counteracts the potential effects of climatic condition change on water temperature and the indirect effects of climatic conditions change such as increased wave action, decreased ice scrape, reduced photosynthetic light intensity (cloudiness) and diminished salinity are more important and potentially affect benthic invertebrates. Practically all our models demonstrated the strong links between salinity and biomass patterns of benthic invertebrates referring to salinity limitation. Most invertebrate species of marine and fresh-water origin live near to their distribution limit in the Gulf of Finland. Therefore reduction in salinity (associated to recent mild winters) has important consequences for these species. As an exception, *S. entomon* is a glacial relict and temperature and ice conditions determined the observed pattern of the species (Leonardsson 1986), whereas the effect of salinity was not significant.

Earlier studies have clearly demonstrated the links between climatic condition variables and zooplankton communities in the Baltic Sea area (Hinrichsen *et al.* 2007) and established the functional relationships between temperature, salinity, species composition and biomass of zooplankton (Ojaveer *et al.* 1998; Vuorinen *et al.* 1998; Möllmann *et al.* 2000). Piontkovski *et al.* (2006) demonstrated that the effect of climatic condition variables on zooplankton community depended on geomorphology of the basin; pelagic communities in small basins responded faster to climatic condition change than those in large basins. In our study we observed significant relationships between environmental variability and zooplankton communities at all scales. Thus, differences in geomorphology of the studied water bodies do not explain the observed patterns of zooplankton communities. More likely, the spatial distribution of zooplankton reflects the east–west gradient in the water circulation patterns of the Gulf of Finland shown by the statistical significance of salinity and spring-time temperature in the models of zooplankton species.

To conclude, our study demonstrated that nutrient loads and climatic condition variables largely explained the observed patterns in benthic and pelagic invertebrate communities. The mobility of organisms determined the relative contribution of small- and large-scale environmental variability to the biomass patterns of invertebrates. Knowledge on the correlation scales between environmental and biotic patterns can provide an insight into how processes generate these patterns. The prevalence of the key processes, however, is further complicated to an unknown extent by regional scale variability. We believe that together with the increase in studies on relationships between nutrient loads, climatic condition variables and biotic patterns at multiple spatial scales and in different regions, meta-analyses (*e.g.* Gurevitch *et al.* 2001) can tackle this problem.

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