Influence of the local abiotic environment, weather and regional nutrient loading on macrobenthic invertebrate feeding groups in a shallow brackish water ecosystem*

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Triin Veber[1]
Jonne Kotta[2,⋆]
Velda Lauringson[1,2]
Ilmar Kotta[2]

[1] Institute of Ecology and Earth Sciences,
University of Tartu,
Vanemuise 46, EE–51014 Tartu, Estonia

[2] Estonian Marine Institute,
University of Tartu,
Mäealuse 10a, EE–12618 Tallinn, Estonia;

e-mail: jonne.kotta@sea.ee

⋆corresponding author

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Abstract

This study evaluated the extent to which depth, sediment type, exposure to waves and coastal slope inclination modulate the relationships between regional nutrient loading, weather patterns and the species composition and dominance structure of macrobenthic invertebrate feeding groups in a brackish water ecosystem of the Baltic Sea. Irrespective of feeding function, the species composition and dominance structure of benthic invertebrate communities were determined by local abiotic

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variables such as exposure, depth and sediment type. Regional weather variables (average southerly winds, salinity, water temperature, ice conditions) either separately or interactively contributed to the variability of benthic invertebrates. Nutrient loading had significant effects on benthic invertebrates only in interactions with local abiotic or regional weather variables. Herbivores, deposit feeders and suspension feeders exhibited a stronger response to the studied environmental variables than carnivores. All this suggests that (1) the dynamic coastal habitats studied in this work are not very sensitive to shifts in nutrient loading and (2) local abiotic conditions and weather patterns largely define the observed biotic patterns. We believe that the benthic invertebrate time series will only be a better reflection of the nutrient loading signal if more years covering extreme events are included.

1. Introduction

Anthropogenic nutrient loading and changes in weather patterns are ranked among the major threats to the structure and functioning of marine coastal communities (e.g. McGowan et al. 1998, Howarth et al. 2000, Jackson et al. 2001). However, the response of a community to forcing of any kind is not straightforward, as it is system attributes that modulate the reaction of the communities (Gray et al. 2002, Kotta et al. 2006a, 2007, Põllumäe et al. 2009). If a certain forcing (for example, nutrient loading) acts to change the communities, mechanisms may be invoked that act to amplify or reduce the effects. Until recently it was believed that coastal eutrophication was controlled primarily by the magnitude of anthropogenic nutrient loading. Recent evidence suggests, however, that changes in weather patterns also affect the nutrient fluxes to the coastal zone (e.g. Justić et al. 2005). There is currently a critical knowledge gap regarding how nutrient loading and weather patterns interactively impact on marine communities and how local system attributes modulate these impacts (Kotta et al. 2009).

The coastal benthic communities in the Baltic Sea are highly dynamic (e.g. Kotta et al. 2008a). Although rising temperatures have caused blooms of benthic invertebrates (Lawrence 1975), the replacement of keystone species (Southward et al. 1995) and other major shifts in the community structure in many European water bodies (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 ecologically unimportant as large seasonal variations counteract the potential effects of recent global warming. On the other hand, the indirect effects of global warming, such as increased wave action, decreased ice abrasion and reduced photosynthetic light intensity (increased cloudiness and turbidity), can be important and potentially affect the structure and function of Baltic coastal communities.

The relationships between the relevant physical and biological processes are as yet insufficiently understood.

The macrozoobenthos represents an intermediate trophic level, and changes in habitat and food conditions affect the structure of benthic communities (Kotta & Orav 2001, Kotta & Møhlenberg 2002, Orav-Kotta & Kotta 2004, Orav-Kotta et al. 2009). Generally, increasing nutrient loads lead to macroalgal blooms and the more intense sedimentation of organic material (Paalme et al. 2002). Enriched food conditions promote higher invertebrate abundances and biomasses (Kotta & Ólafsson 2003, Lauringson & Kotta 2006). Too high a nutrient loading, however, is known to cause hypoxia and irreversible changes in communities (Karlson et al. 2002).

This study aimed to evaluate the extent to which the variability in nutrient loading and weather variables contributed to the abundance and biomass structure of benthic invertebrate feeding groups and how variability in local system attributes modulated these relationships in a shallow brackish water ecosystem of the Baltic Sea.

Our hypotheses were as follows:

(1) The relationship between weather patterns and benthic invertebrate communities is stronger in shallower, exposed areas (< 2 m) than in deeper, sheltered areas (≥ 2 m), because the former areas face stronger disturbances by ice and waves.

(2) The relationship between nutrient loading and benthic invertebrate communities is weaker in shallower, more exposed areas than in deeper, sheltered areas. Strong physical disturbances in shallow exposed areas counteract the effects of nutrient loading, and the accumulating organic matter is constantly resuspended and flushed away to deeper areas. Ice abrasion, on the other hand, periodically removes the excess biomass (e.g. attached macrophytes and sessile invertebrates).

(3) The relationship between nutrient loading and benthic deposit feeders is weaker on bottoms with topographic depressions and humps than on flat sea beds owing to the faster erosion of organic material settling on more complex sea beds (Kotta et al. 2007). Suspension feeders, on the other hand, may benefit from the increased water flow on the more complex bottom topography, as a rising flow velocity improves their food supply, and positive interactive effects between current velocity and phytoplankton biomass are expected (Fréchette et al. 1989, Kotta et al. 2005). Benthic herbivores gain a food supply on a complex bottom topography (increased biomass of attached macrophytes) and also on flat bottoms (enhanced accumulation of drift macrophytes) (Lauringson & Kotta 2006, Kotta et al. 2008c).

(4) Feeding groups at lower trophic levels, such as suspension feeders, deposit feeders and herbivores, display stronger relationships with nutrient loading and weather patterns than organisms at higher trophic levels, such as carnivores.

2. Material and methods

This study was conducted in the shallow semi-enclosed Kõiguste Bay, Gulf of Riga, northern Baltic Sea (58°22.1′N 22°58.7′E). The prevailing sediment type in the bay is sandy clay mixed with pebbles or gravel. The bay varies in depth between 1 m and 7 m and in salinity from 4.5 to 5.5 PSU. The proliferation of ephemeral macroalgae and the appearance of thin drifting algal mats have been reported from the area in recent years, when the principal filamentous algae species in these mats were *Cladophora glomerata* and *Pilayella littoralis* (Lauringson & Kotta 2006, Kotta et al. 2008a).

Figure 1. The study area. The circle indicates the location of the Gulf of Riga and points indicate the locations of the sampling sites with station numbers in Kõiguste Bay (northern Gulf of Riga). Broken lines denote depth contours in metres

The samples were collected with a modified Ekman type bottom grab (0.02 m^2) from 14 sites annually during late July 1998–2006 (Figure 1). Throughout the study GPS was used to locate the stations (accuracy $\pm$ 3 m). Three replicate samples were collected at each station annually. The depth of sampling sites ranged from 0.9 to 6.1 m. The bottom substrates included coarse sand, medium sand and silty sediments. With the use of 0.25 mm mesh screens (see next paragraph) the borderline between fine and medium sands could be accurately delineated; the distinction between other sediment types was made visually. Coarse sand, medium sand and silt were respectively scored as 3, 2 and 1 in the statistical analyses. Hypoxic/anoxic conditions were not observed in the study area during the sampling periods.

Grab samples were sieved in the field on 0.25 mm mesh screens. The residuals 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 species level except for *Hydrobia* spp., oligochaetes, insect larvae and juvenile gammarid amphipods. Ostracods and nematodes were not analysed in the current study. The dry weight of species was obtained after the individuals had been dessicated at 60°C for two weeks. The observed benthic invertebrate species were classified according to their feeding type (suspension feeders, deposit feeders, herbivores, carnivores) on the basis of the literature (Bonsdorff & Pearson 1999) and field observations.

The inclination of the coastal slope was calculated for each station at 1000 m resolutions using the Spatial Analyst tool of ArcInfo software (ArcGIS 9 2004). The calculations were based on the contemporary depth charts (1:1000) available at the Estonian Marine Institute. Higher values of the coastal slope indicate the occurrence of topographic depressions and humps at the measured spatial scale. Values close to zero refer to flat bottoms. The inclination of the coastal slope varied between 0.0005 and 0.0170 degrees.

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

Riverine loading is the most important pathway of nutrients into the Gulf of Riga and exceeds the combined contribution from atmospheric deposition, point emissions from cities and industries along the coast, and nitrogen fixation by marine organisms (Olli et al. 2008). The Gulf receives riverine water from a large drainage area (134 000 km^2), which primarily enters the southern part of the basin. Since the Gulf of Riga is a relatively closed and well-mixed system, the total nutrient load (originating from both Estonian and Latvian shores either as riverine discharge or point emissions) is a good proxy for nutrient conditions in the Kõiguste Bay area. The yearly nutrient load data (total N, total P) for the Gulf of Riga was obtained from the Estonian Ministry of Environment, and the Estonian and Latvian Hydrometeorological Institutes.

As a proxy for atmospheric behaviour the winter index of the North Atlantic Oscillation was used to relate the regional weather 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 connection between the NAO and the wind, temperature and precipitation fields in our study area is strongest during winter. The link between the NAO and sea water temperature may persist over the summer, however, and should be assessed for each site separately (e.g. Ottersen et al. 2001, Jaagus 2006). During the years of high NAO there is a substantial increase in rainfall and, consequently, in freshwater inflow into the Baltic Sea (Hänninen et al. 2000). Elevated pressure differences result in higher winter temperatures in northern Europe (Rogers 1984). In order to get a better understanding of the effects of weather on benthic invertebrate communities, we obtained additional local weather variables such as water temperature, wind patterns, salinity and ice conditions from the Estonian Hydrometeorological Institute.

In the statistical analyses depth, sediment type, exposure to waves and inclination of bottom slope were referred to as the local abiotic environment, loads of total N and P into the Gulf of Riga as nutrient loading variables, and water temperature, wind patterns, salinity, ice condition and the NAO winter index as weather variables. Multivariate data analyses were performed using the PRIMER statistical program, version 6.1.5 (Clarke & Gorley 2006). Invertebrate abundance data were presence-absence transformed to analyse the effect of abiotic variables on the species composition of the benthic communities. Untransformed abundance and biomass data were used to analyse the effect of abiotic variables on the dominance structure of the benthic communities. Abiotic environmental variables were normalised prior to analysis. A global BEST analysis (BIOENV procedure) was used to relate local abiotic, regional weather and nutrient loading variables on the species composition and dominance patterns of benthic invertebrates, separately for different invertebrate feeding groups. In each analysis the separate and combined effects of the studied environmental variables were assessed. The analyses show which environmental variables best explain the observed biotic patterns. Significant interactions between local abiotic, regional weather and nutrient loading variables indicate the key role of the local environment in modulating the effect of regional weather and load patterns. A Spearman rank correlation *r* was computed between the similarity matrices of environmental data (Euclidean distance), species composition and dominance structure of benthic invertebrates. During analyses the dissimilarities of invertebrate communities were quantified by 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). A global BEST match permutation test was run to examine the statistical significance of observed relationships between environmental variables and biotic patterns. The contribution of different species to the differences was calculated by the SIMPER procedure.

3. Results

Altogether 34 taxa were identified in the study area, *Hydrobia* spp., *Macoma balthica* and Chironomidae were the most frequently detected taxa in the study area. *Hydrobia* spp., *M. balthica* and *Cerastoderma glaucum* prevailed in abundance and *M. balthica*, *C. glaucum*, *Theodoxus fluviatilis* and *Mytilus trossulus* in biomass (Table 1).

There was considerable variability in the duration of ice cover and water temperature, but no clear trends could be observed (Figure 2). After 2001, the average wind speed was lower. The probabilities of stormy days (daily average wind speed ≥ 5 m s^{-1}) and calm days (daily average wind speed < 5 m s^{-1}) varied widely on both an annual and a monthly basis. Southerly winds (i.e. those likely to have the greatest impact on the communities of Kõiguste Bay) became less prevalent after 2002. The salinity increased later in the study period. The nitrogen loads into the Gulf of Riga decreased substantially from the late 1990s to the mid-2000s. The loads of total phosphorus varied widely from one year to another and no clear interannual trend was discernible. The respective loads of nitrogen and phosphorus into the Gulf of Riga were estimated at 90 000 and 1 900 t yr^{-1} in the 1990s and 50 000 and 1 700 t yr^{-1} in the 2000s.

When all stations were pooled, deposit feeders, suspension feeders and herbivores were the dominant benthic invertebrate feeding groups in terms of both abundance and biomass. All these feeding groups varied widely year on year, but no clear time trends could be distinguished (Figure 3).

Irrespective of feeding group, the species composition and dominance structure of the benthic invertebrate communities were explained mainly by local abiotic variables such as exposure, depth and sediment type. Regional weather variables (average southerly winds, salinity, water temperature, ice conditions) contributed to the variability in benthic invertebrates either

Table 1. Mean and maximum values of abundance [indiv. m^{-2}], biomass [g d.w. m^{-2}] and occurrence [%] of benthic invertebrate species in Kõiguste Bay

Function	Species	Abundance		Biomass		Occurrence
		mean	max	mean	max	
Deposit feeders	Chironomidae	360	6700	0.120	2.580	85
	Corophium volutator	301	14300	0.119	4.319	38
	Hediste diversicolor	188	1100	0.601	6.420	79
	Leptocheirus pilosus	10	400	0.011	1.040	10
	Macoma balthica	501	2950	12.993	119.615	97
	Marenzelleria neglecta	1	50	0.001	0.094	3
	Oligochaeta	49	1775	0.003	0.086	23
	Pygospio elegans	1	100	0.000	0.004	2
Suspension feeders	*Balanus improvisus*					
	Cerastoderma glaucum	460	19650	5.464	54.020	70
	Mya arenaria	55	3196	1.025	70.155	27
	Mytilus trossulus	108	6600	2.545	134.540	31
Herbivores	*Asellus aquaticus*	30	1000	0.040	2.300	12
	Bithynia tentaculata	19	650	0.528	25.483	15
	Gammarus juv.	113	3050	0.064	1.595	33
	Gammarus oceanicus	6	150	0.010	0.357	7
	Gammarus salinus	35	2700	0.034	0.740	13
	Hydrobia spp.	754	15698	1.809	34.207	100
	Idotea baltica	2	50	0.015	0.409	6
	Idotea chelipes	15	300	0.011	0.205	15
	Idotea granulosa	2	150	0.002	0.115	4
	Jaera albifrons	23	1100	0.014	1.470	13
	Lymnea peregra	19	470	0.142	5.814	14
	Physa fontinalis	6	600	0.004	0.405	3
	Potamopyrgus antipodarum	63	1875	0.279	7.354	25
	Theodoxus fluviatilis	297	3800	2.935	31.650	62
Carnivores	Coleoptera	2	150	0.002	0.095	3
	Corixa	0	50	0.001	0.070	1
	Lepidoptera	0	50	0.001	0.126	1
	Odonata	4	100	0.034	1.315	7
	Piscicola geometra	0	50	0.000	0.020	1
	Prostoma obscurum	23	825	0.004	0.122	21
	Saduria entomon	2	50	0.085	7.850	6
	Trichoptera	5	250	0.004	0.235	4

separately or interactively. Except in suspension feeders, nutrient loading had significant associations with benthic invertebrates only in interactions with local environmental or regional weather variables. The variables contributing most to the models differed among invertebrate feeding groups. Herbivores, deposit feeders and suspension feeders exhibited a stronger response than carnivores (Table 2).

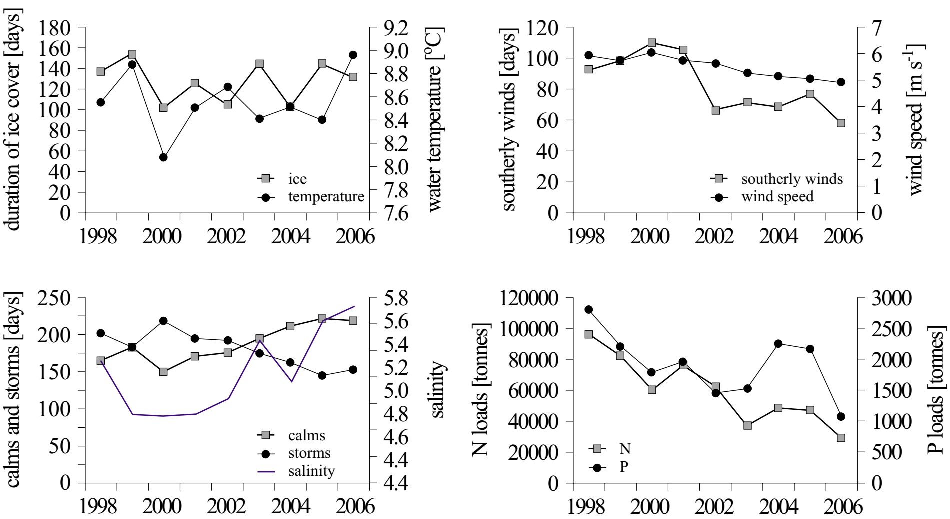

Figure 2. Annual averages of environmental variables in Kõiguste Bay and nutrient load to the Gulf of Riga in 1998–2006

Table 2. Results of BEST permutation (Rho, BIOENV) analysis showing the environmental variables which contribute significantly to explaining the species composition and dominance structure of benthic invertebrate communities. The abbreviations of the variables are as follows: N – total N load, P – total P load, Ice – number of days when Kõiguste Bay is ice-covered, T – water temperature, Sal – water salinity, Exp – exposure to waves, SW – average southerly winds, Sediment – sediment type; '×' denotes the combined effects of the respective variables

Model	Significant environmental variables	Spearman ρ	
Presence			
Carnivores	N×Exp, P×Sal, SW	0.177	0.15
Deposit feeders	Depth, Exp, Ice, P×Exp, N×Sal, P×Ice, SW	0.183	0.01
Herbivores	Depth, Sediment, SW	0.171	0.01
Suspension feeders	Depth, Exp, Sediment, N	0.208	0.01
Abundances			
Carnivores	N×Exp, P×Sal, SW	0.186	0.08
Deposit feeders	Depth, Exp, P×Exp, SW	0.211	0.01
Herbivores	Depth, Sediment, SW	0.157	0.03
Suspension feeders	Depth, Exp, Sediment, N, P×Ice, T	0.179	0.01
Biomasses			
Carnivores	N×Exp, P×Sal, SW	0.160	0.19
Deposit feeders	Depth	0.093	0.10
Herbivores	Depth, Sediment, P×Ice, SW	0.126	0.24
Suspension feeders	Depth, Sediment, N, P×Ice, T	0.148	0.07

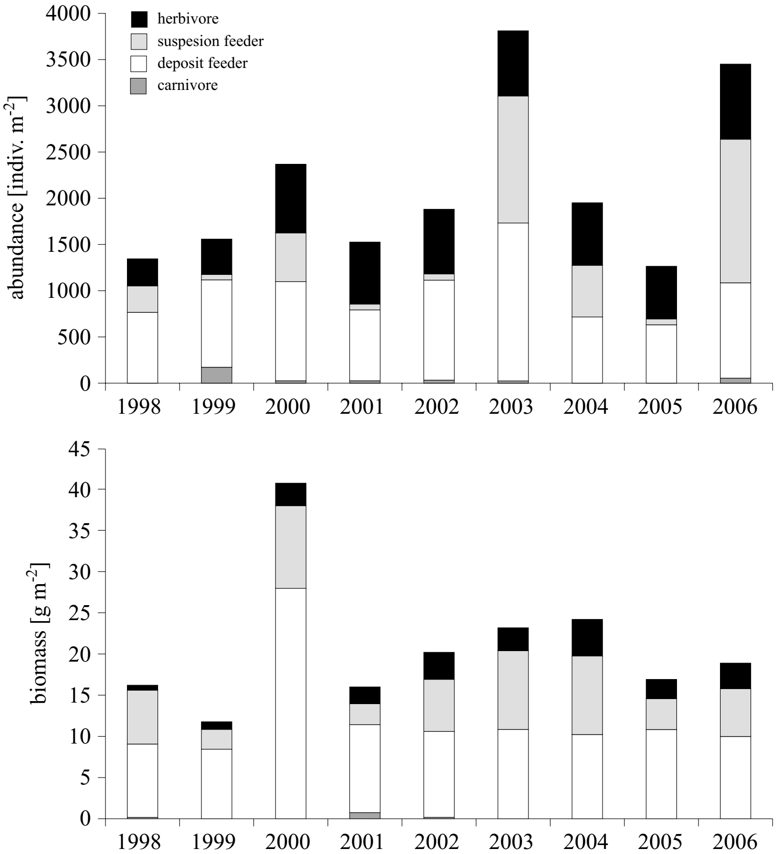

Figure 3. Annual averages of abundances and biomasses of benthic invertebrate feeding groups in Kõiguste Bay in 1998–2006

According to the SIMPER analyses, elevated P loads were correlated with the increased abundance and biomass of herbivores (especially *Hydrobia* spp. and *Potamopyrgus antipodarum*); however, some species such as *Lymnea peregra* and *Gammarus* juv. were depressed, but the effects were strong only under low ice cover. In addition, the abundance and biomass of herbivores were higher on coarser sediments (*Hydrobia* spp., *Idotea chelipes*, *Jaera albifrons*, and *Theodoxus fluviatilis*) and in shallower areas (*Bithynia tentaculata*, *Gammarus salinus*, *Hydrobia* spp., *I. chelipes*, *L. peregra* and *T. fluviatilis*). Herbivores (*I. baltica*, *L. peregra*, *P. antipodarum*) also benefited from southerly winds.

Deposit feeders were favoured by greater depth (*Hediste diversicolor*, *M. balthica*) and stronger southerly winds (*M. balthica*, Oligochaeta, *Leptocheirus pilosus*). The abundance and biomass of deposit feeders decreased with increasing P load, but the effect was stronger at moderate exposure and weaker at reduced and elevated exposure levels (especially *L. pilosus*).

Similarly, the abundance and biomass of suspension feeders increased with depth (*Mytilus trossulus* and *Mya arenaria*). Suspension feeders were favoured by a coarse substrate (*C. glaucum* and *M. trossulus*) and elevated exposure (*M. arenaria* and *M. trossulus*). Suspension feeders were correlated to the nitrogen load either positively (*M. arenaria*) or negatively (*C. glaucum*). However, the abundance and biomass of suspension feeders were the highest at moderate ice cover irrespective of nutrient loads.

Carnivores were favoured by greater exposure (*Saduria entomon*) but only at low and high N loads. The abundance and biomass of carnivores were low at moderate N loads. Carnivores (Coleoptera and Trichoptera) benefited from elevated P loads but only at low salinities and also from increasing southerly winds.

4. Discussion

The aim of this study was to investigate the extent to which regional nutrient loading and weather variables were separately and interactively correlated with the abundance and biomass structure of benthic invertebrate feeding groups and how the local abiotic environment modulated the loading-weather-biota relationships in a brackish water ecosystem of the Baltic Sea. The study showed that local abiotic factors and regional weather variables were largely responsible for the observed patterns of species composition and dominance structure of benthic communities. Nutrient loading also modified local distributions but mainly in interactions with local environmental or regional weather variables.

Sediment type had a significant separate effect on herbivores and suspension feeders irrespective of weather variables and nutrient loading. In general, feeding functions were favoured by the presence of a coarser substrate. Such substrates are known to host more diverse and abundant communities of micro- and macrovegetation and are therefore favourable to herbivores (Fonseca et al. 1990, Edgar et al. 1994). Except for *Mya arenaria*, the benthic suspension feeders studied here use a coarse substrate and/or algae for attachment.

We hypothesised that the relationships between weather variables and benthic invertebrate communities were stronger in shallower than in deeper areas and in exposed than in sheltered areas. Such effects were related mainly to the duration of ice cover and were probably due to the varying intensities of ice abrasion. Ice-mediated effects were observed only in herbivores and suspension feeders, and the effects differed between these feeding groups.

Herbivores benefited from a short period of ice cover. Numerous studies involving the observation or manipulation of natural coastal benthic assemblages indicate that mechanical disturbances, such as ice scouring, and light conditions are essential drivers of macrophyte communities in stressful environments (Heine 1989, Madsen et al. 2001, Schiel 2004, Kotta et al. 2008b, Kotta & Witman 2009), and that the presence of macrophytes directly increases invertebrate species richness and biomass (Fonseca et al. 1990, Edgar et al. 1994, Kotta et al. 2000, 2006b, Edgar & Barrett 2002). It is therefore likely that the disappearance of macrovegetation under severe ice stress explains the inverse relationship between the duration of ice cover and macroherbivores. In addition, floating ice sheets are known to remove the upper (i.e. the most productive) layers of sediment, and thus hinder the development of microherbivores grazing on microphytobenthos (Grall et al. 2006).

Macroalgae are known to outcompete benthic suspension feeders at shallow depths, and lush macrophyte communities are therefore often characterised by low densities of suspension feeders (Janke 2006). Moderate ice disturbance partly removes the algal carpet, thus releasing benthic suspension feeders from such interspecific competition (Kotta & Witman 2009). Too great an ice disturbance, however, also removes most suspension feeders. This may explain why suspension feeders benefited from moderate ice disturbance and why their densities were low when the duration of ice cover was either very short or very long.

Wind variables did not interact with any of the environmental variables studied. Irrespective of depth and exposure levels, southerly winds had separate, strong effects on all functional groups of benthic invertebrates except suspension feeders. The southerly winds were beneficial to all invertebrate functions, suggesting that there is a generic link between southerly winds and the trophic status of the bay. Strong southerly winds increase seawater temperature and therefore enhance the growth of most benthic invertebrates (Phillips 2005). In addition, southerly winds bring in a lot of organic debris that is channelled directly or indirectly to different invertebrate feeding groups (Tomczak et al. 2009).

Many recent studies have used different NAO indices as a proxy of climate patterns in the northern hemisphere in order to assess the effects of climate change on local communities (Ottersen et al. 2001, Stenseth et al. 2002, Kotta et al. 2004a). In this study we used the NAO winter index (December–March) together with local weather variables. The index was highly correlated with the period of ice cover, winter mean temperature, storminess, precipitation and light conditions (cloudiness) in our study area (Jaagus 2006 and this study). With decreasing values of the NAO index local communities were more likely to suffer under more severe mechanical disturbances due to ice scouring coupled with the poorer light regime. As seen in our models local weather variables were very powerful in explaining the dynamics of different benthic invertebrate functions, and the addition of the NAO index did not improve the descriptive power of the models. Thus, future studies that aim to establish relationships between weather patterns and biota should include local weather variables to improve the model fit and to acquire a mechanistic insight into the processes involved.

We also hypothesised that the relationship between nutrient loading and benthic invertebrate communities would be weaker in shallower, exposed areas than in deeper, sheltered areas. Although nutrient loading did modify local distributions, mainly in interactions with local environmental variables, this hypothesis did not hold true. In fact the response of deposit feeders to nutrient loading was highest at moderate exposure, as was that of carnivores at shallower depths. On the other hand, herbivores benefited from elevated nutrient loadings only when ice disturbance was minimal.

It has been demonstrated that elevated eutrophication results in blooms of opportunistic macroalgae and the development of drifting algal mats in the Baltic Sea (Berglund et al. 2003). The algal mats are known to accumulate in moderately exposed areas (Kotta et al. 2008c), where they provide a habitat and food for benthic invertebrates (Kotta et al. 2004b, 2008c, Orav-Kotta & Kotta 2004). Although the spring detrital pulse explains a large part of the annual offshore benthic production (Levinton & Stewart 1988, Ólafsson & Elmgren 1997, Pasternack & Brush 2001), coastal macroinvertebrates nowadays clearly take advantage of the greater biomasses of drifting macroalgae as an important source of nutrients all the year round (Thiel & Watling 1998, Kotta et al. 2008a). As the biomasses of drifting algae exceed many times those of attached algae, the responses of associated invertebrates are expected to be strong at the sites where the algal mats accumulate.

We further hypothesised that suspension feeders would benefit from the increased nutrient loading on a complex seabed as elevated flow velocity and phytoplankton biomass interactively increases their food supply. In reality the response of suspension feeders to nutrient loading was complex (Lauringson et al. 2009). Some species profited from N loading whereas other species were harmed, producing an overall negative effect on benthic suspension feeders. Ice cover overrode the effect of P loading as the highest abundances and densities of benthic suspension feeders were observed at moderate ice disturbance, irrespective of the P loadings. This suggests that some bivalves (*Cerastoderma glaucum*) are not food limited in our study area, whereas others (*Mya arenaria*) are often depleted of suspended particulate matter; increasing phytoplankton biomasses can reverse this food limitation (Kotta et al. 2005, Lauringson et al. 2007). An inverse relationship between nutrients and, say, *C. glaucum* indicates that nutrient loading indirectly (e.g. through clogging, hypoxia and smothering by drifting algae) reduces the populations of suspension feeders in the study area. Strong physical disturbances in shallower sites (e.g. due to ice abrasion) seem to completely counteract the effects of nutrient loading. Only at moderate physical disturbance levels does the accumulating organic matter impact local communities since it is not flushed away to deeper areas.

We expected feeding guilds at lower trophic levels to display stronger relationships with nutrient loading than organisms at higher trophic levels. Indeed, herbivores and deposit feeders showed stronger responses than carnivores. However, suspension feeders were as weakly related to nutrient loading as carnivores. Factors affecting deposit feeders and herbivores seem to operate locally, whereas suspension feeders are simultaneously affected by basin-wide effects on phytoplankton and by local factors such as the availability of resuspended microphytobenthic cells or detritus; moreover, large-scale effects can often override small-scale effects (Sauriau & Kang 2000, Kasim & Mukai 2006, Sarà 2006). Basin-wide and local effects can to some extent even counteract each other: for instance, frequent storms can promote phytoplankton blooms via upwelling events but carry away detrital material locally, and stormy weather or large-scale phytoplankton blooms can in turn result in reduced light conditions, which may locally suppress the development of benthic microalgae. Such complicated sets of effects may partially explain the observed weak relations between nutrient loading and suspension feeders. Carnivores represent a higher trophic level and are not necessarily controlled by bottom-up effects (Posey et al. 1995, Põllumäe & Kotta 2007). This can explain why the effects of nutrient loading and weather on carnivores in general did not depend on the local abiotic environment.

To conclude, the species composition and dominance structure of benthic invertebrate communities were determined by local abiotic variables. Regional weather variables either separately or interactively contributed to the variability of benthic invertebrates. Nutrient loading had significant effects on benthic invertebrates only in interactions with local abiotic or regional weather variables. Our results suggest that the harsh and dynamic coastal habitats of the Baltic Sea are not very sensitive to shifts in nutrient loading. It has been speculated that the benthic invertebrates inhabiting the dynamic Baltic Sea are highly adaptive and very resistant to any physical and biological disturbances (Jernelöv & Rosenberg 1976, Herkül et al. 2006). Such weak responses may be due to the opportunistic characteristics of benthic species in the study area (Kotta et al. 2008a). The regions that have high shares of mobile and opportunistic species are expected to be more resistant to changes in nutrient loading than regions characterised by perennial, long-living and sessile species (Cloern 2001, Posey et al. 2006, Kotta et al. 2007). We believe that the benthic invertebrate time series will only be a better reflection of the nutrient loading signal if more years covering extreme events are included.

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