

The structure and dynamics of zooplankton communities in shallow bays in the northern Baltic Sea during a single growing season

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The littoral zone forms a large proportion of the northern Baltic Sea and creates diverse and prolific habitats with high regional importance. However, our understanding of the structure and functioning of littoral food webs is constricted, because their zooplankton communities remain virtually unstudied. We investigated variability in the structure and dynamics of littoral zooplankton communities, in relation to landscape-level gradients in environmental conditions, in four shallow bays in the Åland archipelago during one growing season. The variability was best explained by the productivity potential, i.e. the concurrent effects of temperature, trophic state, and phytoplankton biomass, of the environment. Zooplankton abundance and biomass showed a significant, positive correlation with these factors. Also the structure of zooplankton communities and their seasonal succession patterns were strongly associated with productivity potential. In general, the littoral zooplankton communities were characterized by higher diversity and abundance, and earlier succession patterns than previously reported for the northern Baltic pelagial.

Introduction

Ecosystems are regulated by the interplay between the cascading effects of bottom-up and top-down forces (Hairston *et al.* 1960). Zooplankton plays a pivotal role as a structural and functional mediator in marine (Banse 1995) and freshwater ecosystems (Lampert 1997, Scheffer 1998). It has a central position in aquatic food webs constituting a major trophic link between a myriad of primary producers and higher consumers (Pomeroy 1974, Steele 1998). Due to the numerous connections, zooplankton communities are intimately involved in a vast range of fun-

damental ecosystem processes and mechanisms shaping the abiotic and biotic environment.

Zooplankton grazing drives the vertical particle flux in the water column (Kjørboe 1998). This affects the distribution of available nutrients, and thus the composition and distribution of benthic and pelagic organisms. Herbivorous zooplankton may shape the composition of phytoplankton communities (Brett *et al.* 1994, Sommer *et al.* 2001) and can even limit their total productivity (Brooks and Dodson 1965, Jeppesen *et al.* 1990, Muylaert *et al.* 2006). Furthermore, in shallow habitats, herbivorous zooplankton can regulate the balance between regimes dominated by

either phytoplankton or macrophytes (Jeppesen *et al.* 1998, Scheffer 1998, Perrow *et al.* 1999). Possible shifts between such regimes are consequential for the whole ecosystem structure (e.g. Österblom *et al.* 2007). As a source of food, zooplankton is important for pelagic and benthic invertebrates (Albertson and Leonardson 2001, Viherluoto and Viitasalo 2001) and for fish (Mehner and Thiel 1999, Elliott and Hemingway 2002). The availability of suitable zooplankton at the right time and place is particularly crucial for fish larvae (Cushing 1990). In addition to predation, this kind of matching is considered the most important factor controlling the cohort strength in many fish populations (Mehner and Thiel 1999, Lenz in Harris *et al.* 2000). Consequently, zooplankton can have long-term effects on the demography of fish populations (Flinkman *et al.* 1998, Rothschild 1998) and on the composition and productivity of entire fish communities (Werner and Hall 1988, Arrhenius 1996, Hakala *et al.* 2003).

The northern Baltic Sea is characterized by its vast mosaic-like archipelagos consisting of thousands of small islands. Due to the planar profile of the region and the extensive length of the aggregate shoreline, a large proportion of the northern Baltic is covered by shallow bottoms. These littoral areas constitute prolific habitats and are thus of large importance for the biota in the whole northern Baltic. Despite the extensive ecological research in this region during the recent decades, littoral zooplankton communities remain rudimentarily studied. We confronted this gap of knowledge by surveying the structure and dynamics of zooplankton communities in flads, i.e. shallow bays with an opening threshold (Ingmar 1975, Munsterhjelm 1997, 2005). In this text, zooplankton refers to all rotifers, cladocerans and copepods, which have been caught in a 50 μm plankton net. Hence, besides mesozooplankton (200–2000 μm), larger individuals of microzooplankton (20–200 μm) are included in this study. Flads are, for several reasons, applicable models for assessing general variability in littoral zooplankton communities in the northern Baltic Sea. Firstly, flads represent a wide range of environmental conditions at the landscape level (Appelgren and Mattila 2005, Hansen 2007). Secondly, they are, in the marine

context, distinctive ecological units with rather clear-cut physical boundaries. The structures of flad communities can thus be utilized to assess community patterns associated with regional gradients in environmental conditions.

Several features, such as topography, the composition of macrophytes and habitat structure, are common for flads and shallow temperate lakes (Scheffer 1998). However, there are also clear differences mainly due to higher salinity and the connection to the surrounding sea areas influencing the ecosystem structure and dynamics in the flads. The trophic state or the productivity potential is regarded as a major regional determinant for the composition of zooplankton in both lakes (Barnett and Beisner 2007) and in the pelagic areas of the northern Baltic (Johansson 1992). Additionally, salinity fundamentally shapes the structure of zooplankton communities in the pelagic areas of the northern Baltic (Viitasalo 1994, Dippner *et al.* 2001). In this brackish water estuary, the biota consists of a mixture of species with marine and freshwater origin.

We surveyed the structure and seasonal dynamics of zooplankton communities in relation to environmental variables in mesotrophic and eutrophic flads exhibiting low and high water temperatures during the growing season. The selected sites typify both ends of the regional gradients in productivity potential (Snickars *et al.* 2009). For the sake of simplicity, the flads with low and high productivity potential will hereafter be referred to as mesotrophic and eutrophic, respectively. This means that in this context also temperature is included as a factor in respective term. The primary objective of the study was to compare the abundance and diversity of zooplankton communities and to relate the observed patterns to abiotic, environmental variables and biomass of phytoplankton. Based on information from the pelagic areas of the northern Baltic and shallow temperate lakes, we proposed three basic hypotheses on the structure of the surveyed zooplankton communities: (1) the abundance and biomass of zooplankton are significantly higher at the eutrophic than at the mesotrophic sites; (2) the diversity and richness of zooplankton are significantly higher at the mesotrophic than at the eutrophic sites; (3) the composition of the communities differs significantly more between

than within the mesotrophic and the eutrophic sites. We shall also verify whether the hypothesized patterns are, in fact, mainly attributable to the stated premises, i.e. environmental conditions shaped by the productivity potential. Our results should enable an assessment of the variability of littoral zooplankton communities in relation to fundamental gradients in environmental conditions in the northern Baltic Sea. Furthermore, the results ought to provide for a prolific framework for studying landscape level patterns in the composition of communities.

Material and methods

Study sites and schedule

The study was carried out during the growing season 2003 in four flads in the archipelago of Åland Islands, in the northern Baltic Sea. The year was well representative with respect to weather conditions. The sites were chosen among 20 flads located in the Åland Islands. The large array of flads had been surveyed for abiotic and biotic conditions during the previous growing season (Snickars *et al.* 2009). All sites were then ordered according to gradients in environmental conditions. Two of the selected sites, the mesotrophic Hamnflada and Norrflada, epitomized flads with low productivity potential. The other two, the eutrophic Mjärdvik and Notgrund, were characteristic for the opposite end of the productivity gradient. Thus, the survey sites were chosen to cover a wide range of the factors expected to be relevant in shaping the structure of littoral zooplankton communities. However, sites with extreme environ-

mental conditions were avoided, and low exposure to human-induced influence was preferred (Table 1). Furthermore, the survey schedule was designed to encompass maximal temporal variability expressed in the community structure. The sites were surveyed seven times during the growing season (weeks 19, 22, 24, 26, 30, 33 and 36).

Environmental variables

Data on the environmental variables originate from an EU/Interreg IIIA project "Production of juvenile fish in shallow bays" (J. Mattila unpubl. data). Depth was measured in the field with 0.1 m accuracy. Other morphological characteristics, i.e. opening area, bay area, shoreline length and catchment area of the sites were calculated from maps. The exposure index value is the quotient of the opening cross-section and the bottom area $\times 100$ (Appelgren and Mattila 2005).

Temperature at each survey site was measured with the Gemini TinyLogger™ log devices at ca. 1-m depth at 2-h intervals throughout the season. Water samples for analysis of salinity, turbidity, total phosphorus, total nitrogen and chlorophyll *a* were taken from 0.5-m depth in the middle of each bay. Except for the nutrients, which were not investigated during the weeks 22 and 36, other environmental variables were measured during each survey.

Zooplankton

Three replicate samples of zooplankton were taken in the middle of each site between 09:00

Table 1. Geographical, topographical and morphological characteristics, i.e. stable environmental parameters for each survey site.

Site	Hamnflada	Mjärdvik	Norrflada	Notgrund
N coordinates (WGS-84)	60°17'493	60°17'773	60°05'343	60°15'910
E coordinates (WGS-84)	20°19'733	19°46'282	20°17'849	19°51'170
Archipelago zone	middle	middle	middle	inner
Catchment area (m ²)	103813	269223	160112	506463
Succession stage	juvenile flad	glo-flad	flad	flad
Exposure index value	0.31	0.02	0.23	0.04
Average bay depth (m)	1.2	2.1	2.1	1.2

and 12:00. The whole water column (1.8–3.0 m) was evenly and completely covered with a Limnos sampler (height = 40 cm, diam. = 9 cm, vol. = 2.6 l). The sampler was lowered to predefined depths, related to the total depth of each sampling site. The total volume of each replicate was 18.2 l. The samples were filtered through a 50 μm plankton net concentrating the final volume to 80 ml. The samples were stored in 5% formalin solution.

Due to high zooplankton densities in most samples, subsamples had to be taken. The samples were divided into halves with a Folsom splitter until a suitable density for examination was reached. The adequate subsamples were then placed in 10 ml cuvettes for analysis with a phase-contrast microscope. Individuals were identified to the lowest possible taxonomical level. Further, the life stage of copepods was documented as nauplii, juveniles or adults. Only the adults were identified to the species or genus level. The resulting categories, based on the taxonomy and/or life stage of the specimens, are hereafter referred to as groups. Consequently, the number of species in a group is one or more depending on the accuracy of the identification. In most samples, approximately 1000 specimens were analyzed. In few sparse samples, at least 500 specimens could still be examined. Additionally, the lengths of the 20 first encountered specimens within each group were measured according to Harris *et al.* (2000). The results were not corrected for shrinkage.

Numerical analyses

Four universal variables — (1) total abundance, (2) total biomass, (3) group richness and (4) group diversity — were used to describe and compare the zooplankton communities. Further, two solely relative measures — (5) the number of groups in common and (6) Bray-Curtis similarity index (Bray and Curtis 1957, Gauch 1973) — were applied for comparisons between each pair of sites. The first two variables describe the quantity of zooplankton communities, the two following ones are measures of α -diversity, and the last two reflect the β -diversity (Whittaker 1972) of the communities.

The abundance (ind. l^{-1}) of each zooplankton group was measured from the samples. The values were then converted into biomass ($\mu\text{g l}^{-1}$ wet weight) according to Hernroth (1985), Viitasalo (1992) and unpublished calculations done at the Finnish Institute of Marine Research, and based on the length measurements.

As all the specimens could not be identified to the species level, group richness (S), i.e. the total number of groups, was used as a surrogate variable for the more conventional species richness. Similarly, Shannon's diversity index (Shannon 1948) values (H') were calculated to represent the diversity of zooplankton groups in the samples. The index takes into account the number of species and the evenness of their abundances. The index value increases in tandem with the values of these two parameters (Krebs 1989).

Number of groups in common (for each pair of sites) and Bray-Curtis similarity index (also referred to as Czekanowski and Sørensen indices) were applied to describe the relative structure of zooplankton communities. Percentage (0%–100%) of groups in common for each pair of sites was calculated from presence/absence data. By contrast, Bray-Curtis similarity index values were calculated from non-transformed data to take into consideration the full-scale variability in the composition of zooplankton communities. The Bray-Curtis index reflects differences between two samples based on differences in community composition and/or total abundance. The measure is not affected by species that are absent from both of the compared samples. When two samples are identical, the similarity measure is 100% and when they have no species in common, similarity is 0% (Eleftheriou and McIntyre 2005).

On top of the six community-level variables, the abundance and biomass proportions of individual zooplankton groups are reported as percentages. In addition to a descriptive presentation of the seasonal dynamics of the most abundant groups, group-specific data are used in supplementary purpose to explain patterns in the community-level variables.

The distributions of the universal variables (1–4) were tested for normality with a Kolmogorov-Smirnov test and for homogeneity of variances with Levene's test. After concluding

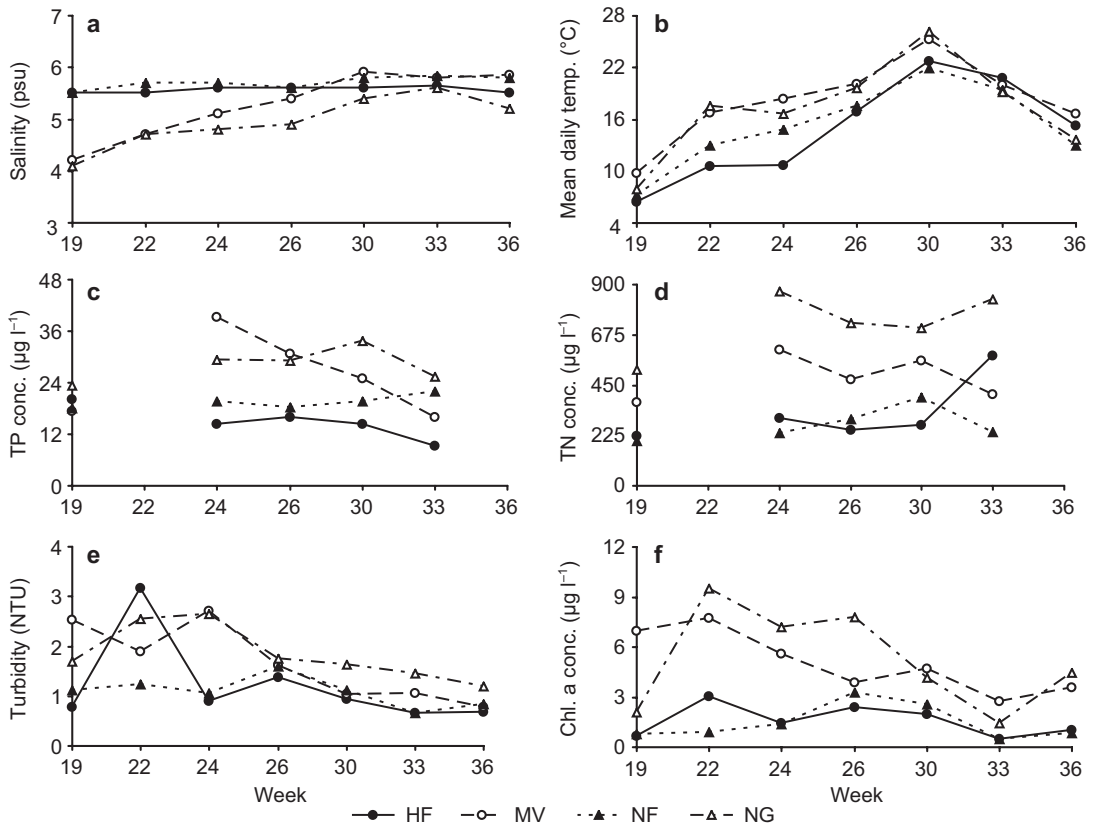


Fig. 1. Abiotic, environmental variables and chlorophyll *a* concentrations from May to September 2003: (a) salinity (psu), (b) mean daily temperature (°C), (c) concentration of total phosphorus ($\mu\text{g l}^{-1}$), (d) concentration of total nitrogen ($\mu\text{g l}^{-1}$), (e) turbidity (NTU), and (f) concentration of chlorophyll *a* ($\mu\text{g l}^{-1}$). Note that the scales for salinity and mean daily temperature do not start from zero. HF = Hamnflada, MV = Mjårdvik, NF = Norrflada and NG = Notgrund. The closed and open symbols represent the mesotrophic and eutrophic sites, respectively. The high turbidity value in Hamnflada during week 22 is supposedly an artefact.

that all assumptions for parametric tests were met, two-way (site \times occasion) ANOVA was applied to examine the relative extent of spatial and temporal sources of variation in the zooplankton community structure. The attendant pair-wise comparisons were done using the Holm-Sidak test. Moreover, one-way ANOVA followed by Tukey's HSD post-hoc test were employed to separately examine the spatial and temporal components of variation. The latter combination of analyses was also applied to compare the sites with each other, with respect to whole-season values (averages or sums) for the four universal variables (Underwood 1997).

Pearson's correlation was used to examine the relationship between the community variables 1–4 and total phosphorus, total nitrogen,

salinity, temperature, turbidity and chlorophyll *a*. Average values for each site were used for the different variables.

Results

Environmental variables

The measured environmental variables exhibited patterns that conformed to the premised classification of the study sites into ones with low and high productivity potential (Fig. 1). All measured, productivity-related, environmental variables showed congruent seasonal dynamics. In general, the largest differences between the mesotrophic and eutrophic sites were found from

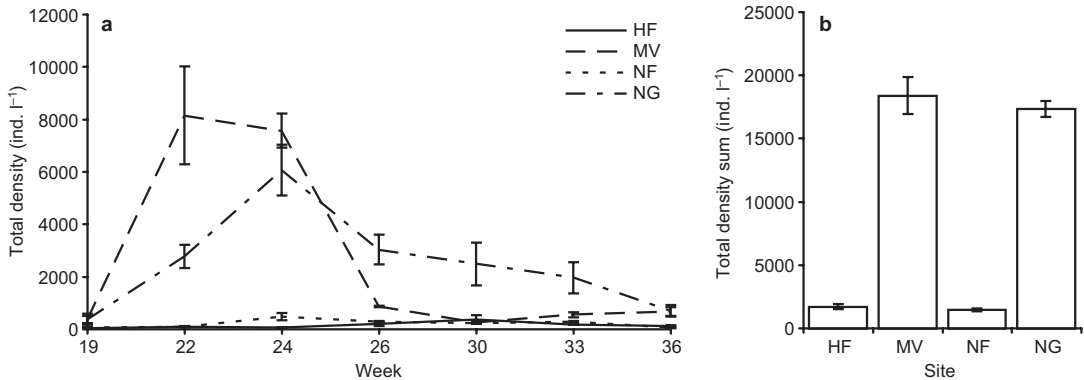


Fig. 2. (a) Zooplankton abundance (ind. l⁻¹) in the study sites from May to September 2003. (b) Total zooplankton abundance in the study sites (ind. l⁻¹). HF = Hamnflada (mesotrophic), MV = Mjärdvik (eutrophic), NF = Norrflada (mesotrophic) and NG = Notgrund (eutrophic).

late May until early June. Salinity was slightly higher at the mesotrophic than in the eutrophic sites until the end of July (Fig. 1a). Thereafter no differences between the site types could be observed. The mean daily temperature was lower at the mesotrophic than at the eutrophic sites throughout the season (Fig. 1b). The differences were most prominent until the beginning of August. Similar patterns applied to the dynamics in the concentrations of total phosphorus and nitrogen (Fig. 1 panels c and d, respectively). Further, the eutrophic sites were characterized by relatively higher water turbidity (Fig. 1e). However, the differences in turbidity between the site types were almost levelled off by mid-July. Finally, the concentration of chlorophyll *a* was remarkably higher at the eutrophic than at the mesotrophic sites during every sampling event (Fig. 1f). However, ephemeral, lower differences between the site types were observed in August.

Zooplankton

Zooplankton quantity

Zooplankton abundance dynamics did not coincide between the sites (Fig. 2). This was indicated by the significant interaction between the spatial and temporal components of variation in the two-way ANOVA ($F_{18,56} = 32$, $p < 0.001$) (Table 2). At the eutrophic sites, the highest abundance appeared in late spring and early summer, whereas in the mesotrophic sites abun-

dance was highest around July. The whole-season sum of zooplankton abundance was about ten times higher at the eutrophic than at the mesotrophic sites (one-way ANOVA: $F_{3,8} = 411$, $p < 0.001$; Table 2; Tukey HSD: $p < 0.001$), whereas the differences within a respective site type were low and insignificant. At both eutrophic sites, the highest abundances were mainly attributable to substantial numbers of *Keratella cochlearis* and *Keratella quadrata*. At the mesotrophic sites, *Synchaeta* spp. and calanoid nauplii were, in turn, the most dominant groups during the abundance peaks. Further, high occurrence of *Keratella cochlearis* was associated with high total abundances also at these sites (Fig. 3).

Similar to abundance, the zooplankton biomass dynamics differed between the sites (two-way ANOVA/interaction: $F_{18,56} = 28$, $p < 0.001$; Table 2) (Fig. 4). Peaks occurred somewhat earlier at the eutrophic than at the mesotrophic sites. Moreover, a notable second biomass peak was observed in Notgrund in mid-August. The whole-season sum of zooplankton biomass was considerably higher at the eutrophic sites, Mjärdvik ($6221 \mu\text{g l}^{-1}$) and Notgrund ($6773 \mu\text{g l}^{-1}$) than at the mesotrophic sites, Hamnflada ($1435 \mu\text{g l}^{-1}$) and Norrflada ($2744 \mu\text{g l}^{-1}$). According to the one-way ANOVA ($F_{3,8} = 1441$; $p < 0.001$; Table 2) and Tukey's HSD test, the differences between (Hamnflada vs. Mjärdvik, Hamnflada vs. Notgrund, Mjärdvik vs. Norrflada and Norrflada vs. Notgrund: $p < 0.001$) and within (Hamnflada vs. Norrflada: $p < 0.001$, Mjärdvik vs. Notgrund: $p = 0.002$) the mesotrophic

and eutrophic site types were significant. At the eutrophic sites, mainly *Keratella cochlearis*, *Keratella quadrata*, *Synchaeta* spp. and different life stages of cyclopoids were responsible for the high biomass levels in late spring and early summer. During the later biomass peak in Notgrund, almost 80% of zooplankton biomass

consisted of *Synchaeta* spp. At the mesotrophic sites, the peaks in biomass were mainly attributable to *Synchaeta* spp. and different life stages of calanoids. In general, zooplankton biomass was more evenly distributed between different groups at the eutrophic sites than at the mesotrophic ones (Fig. 5).

Table 2. ANOVA results for the four universal variables. The two-way ANOVA is applied on all sampling occasions and sites, whereas the one-way ANOVA compares the sites with each other by using whole-season values.

Variable	Source	SS	df	MS	F	p
Total density (ind. l ⁻¹)						
Two-way ANOVA						
	Spatial	123.239	3	41.080	560.788	< 0.001
	Temporal	37.185	6	6.198	84.604	< 0.001
	Interaction	41.891	18	2.327	31.770	< 0.001
	Residual	4.102	56	0.073		
	Total	206.418	83			
One-way ANOVA						
	Between sites	798346979.634	3	266115659.878	411.369	< 0.001
	Within sites	5175217.015	8	646902.127		
	Total	803522196.650	11			
Total biomass (µg l ⁻¹)						
Two-way ANOVA						
	Spatial	52.261	3	17.420	305.047	< 0.001
	Temporal	34.015	6	5.669	99.271	< 0.001
	Interaction	28.761	18	1.598	27.979	< 0.001
	Residual	3.198	56	0.057		
	Total	118.235	83			
One-way ANOVA						
	Between sites	61313294.657	3	20437764.886	1441.168	< 0.001
	Within sites	113451.132	8	14181.392		
	Total	61426745.791	11			
Group richness (S)						
Two-way ANOVA						
	Spatial	55.286	3	18.429	4.807	0.005
	Temporal	250.310	6	41.718	10.883	< 0.001
	Interaction	124.548	18	6.919	1.805	0.048
	Residual	214.667	56	3.833		
	Total	644.810	83			
One-way ANOVA						
	Between sites	6.517	3	2.172	3.397	0.074
	Within sites	5.116	8	0.639		
	Total	11.633	11			
Group diversity (H')						
Two-way ANOVA						
	Spatial	0.296	3	0.099	35.300	< 0.001
	Temporal	0.570	6	0.095	33.936	< 0.001
	Interaction	0.879	18	0.049	17.447	< 0.001
	Residual	0.157	56	0.003		
	Total	1.901	83			
One-way ANOVA						
	Between sites	0.103	3	0.034	67.249	< 0.001
	Within sites	0.004	8	0.001		
	Total	0.107	11			

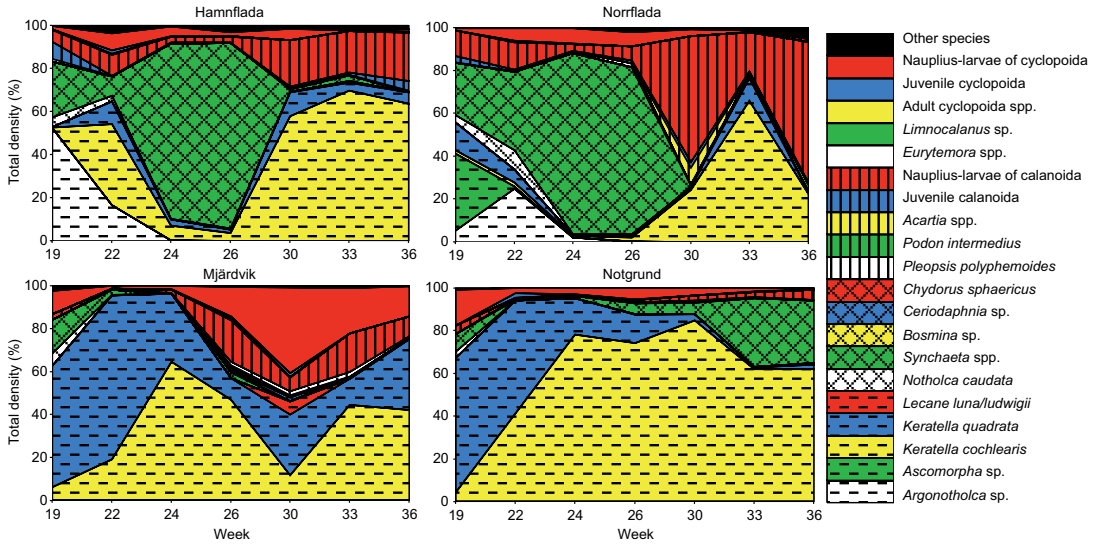


Fig. 3. Percentages of different zooplankton groups of the total zooplankton abundance (ind. l⁻¹) at the survey sites from May to September 2003. Only groups contributing more than 5% to the total abundance or biomass at least at one site and on one occasion were included in the figure as separate groups. All the other groups are pooled under “other species”. Hamnflada and Norrflada are mesotrophic, whilst Mjärdvik and Notgrund are eutrophic sites.

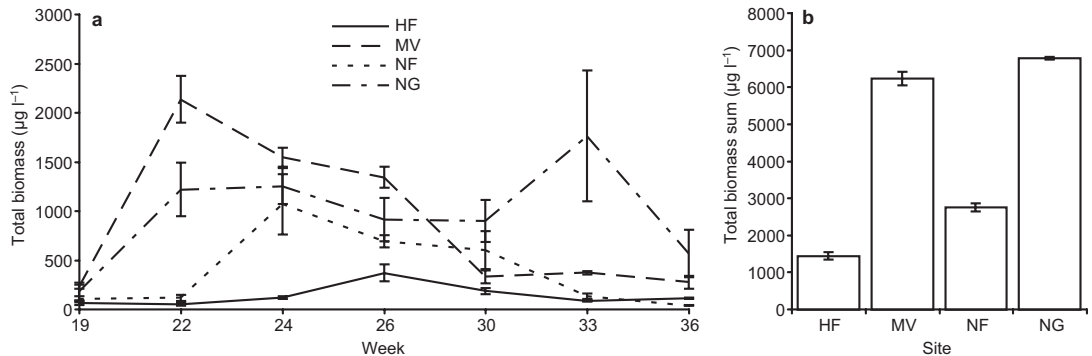


Fig. 4. (a) Dynamics of zooplankton biomass (µg l⁻¹ [wet weight]) at the study sites during the survey season. (b) Seasonal sum of zooplankton biomass at the study sites (µg l⁻¹ [wet weight]). HF = Hamnflada (mesotrophic), MV = Mjärdvik (eutrophic), NF = Norrflada (mesotrophic) and NG = Notgrund (eutrophic).

Zooplankton α -diversity

Group richness was quite similar at all sites with the highest values observed around midsummer (Fig. 6). Even though the interaction between the spatial and temporal components of variation was significant (two-way ANOVA: $F_{18,56} = 2$, $p = 0.048$; Table 2), no clear pattern which could be attributed to the mesotrophic and eutrophic site types was found. The number of groups encountered during the whole season ranged from a total of 29 in Norrflada to 38 in Mjärdvik

(one-way ANOVA: $F_{3,8} = 29$, $p < 0.001$; Table 2), resulting in a total number of 55 groups for the whole survey. According to Tukey's HSD post-hoc test, only the group richness values in Norrflada differed significantly from the ones at the other sites (Hamnflada: $p = 0.001$, Mjärdvik: $p < 0.001$ and Notgrund: $p = 0.006$). The turnover of groups was rapid at all sites. At highest, only half of the groups encountered at a given site during the whole season were present on any single occasion. Four species, *Keratella cochlearis/recurvispina*, *Synchaeta cecilia*, *Podon*

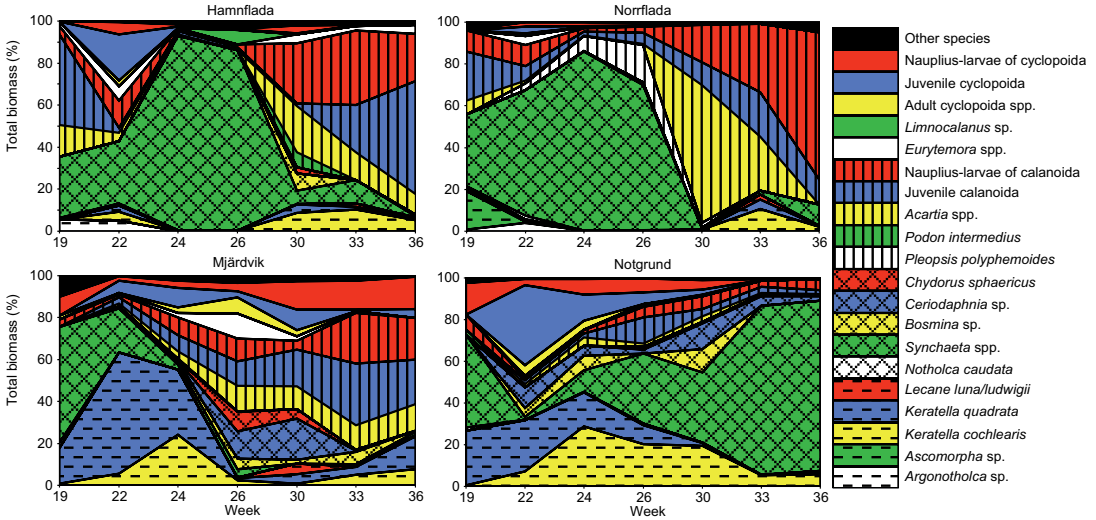


Fig. 5. Percentages of different zooplankton groups of the total zooplankton biomass ($\mu\text{g l}^{-1}$ wet weight) at the survey sites from May to September 2003. Only groups contributing more than 5% to the total abundance or biomass at least at one site and on one occasion were included in the figure as separate groups. All the other groups are pooled under “other species”. Hamnflada and Norrflada are mesotrophic, whilst Mjärdvik and Notgrund are eutrophic sites.

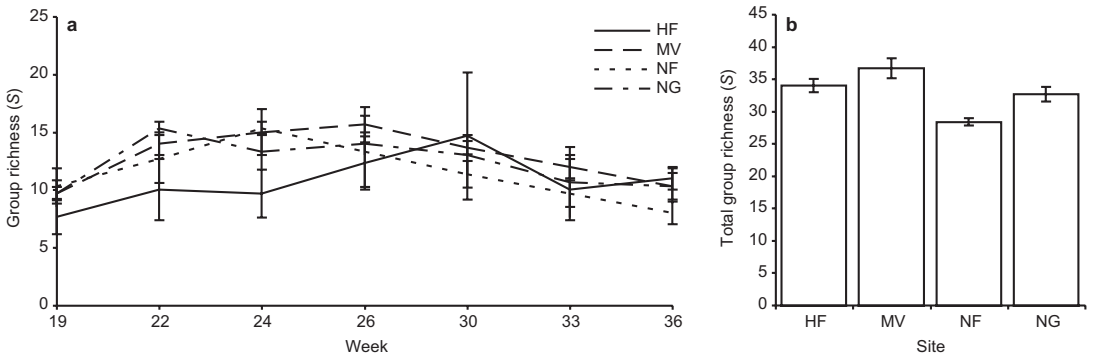


Fig. 6. (a) Dynamics of zooplankton group richness (S) at the study sites during the survey season. (b) Total zooplankton group richness at the study sites (S). HF = Hamnflada (mesotrophic), MV = Mjärdvik (eutrophic), NF = Norrflada (mesotrophic) and NG = Notgrund (eutrophic).

leuckarti and *Limnocalanus* sp. were unique to Hamnflada. Three species, *Brachionus urceus*, *Rotatoria rotatoria* and *Diaphanosoma brachyurum*, were encountered only in Mjärdvik. Also Notgrund harboured three species, *Keratella quadrata/platei*, *Synchaeta litoralis* and *Alona* sp., unique to the site. Norrflada had only one species, *Cephalodella* sp., absent in all the other sites. Shannon’s diversity index values varied from 0.24 to 0.84 (Fig. 7a). The interaction between the spatial and temporal components of variation was highly significant (two-way ANOVA: $F_{18,56} = 17$; $p < 0.001$), displaying the

lack of general, spatial or temporal trends (Table 2). Accordingly, the sites differed significantly from each other on most occasions. Also the differences in whole-season average values were significant (one-way ANOVA: $F_{3,8} = 67$, $p < 0.001$; Table 2) (Fig. 7b). However, no clear distinction could be made between eutrophic and mesotrophic sites. Hamnflada had the highest average value of Shannon’s diversity index, 0.65 ± 0.03 . Tukey’s HSD post-hoc test indicated a significant difference between this value and the ones for Mjärdvik ($p = 0.02$), Norrflada (0.54 ± 0.01 , $p = 0.001$) and for Notgrund (0.52 ± 0.02 ,

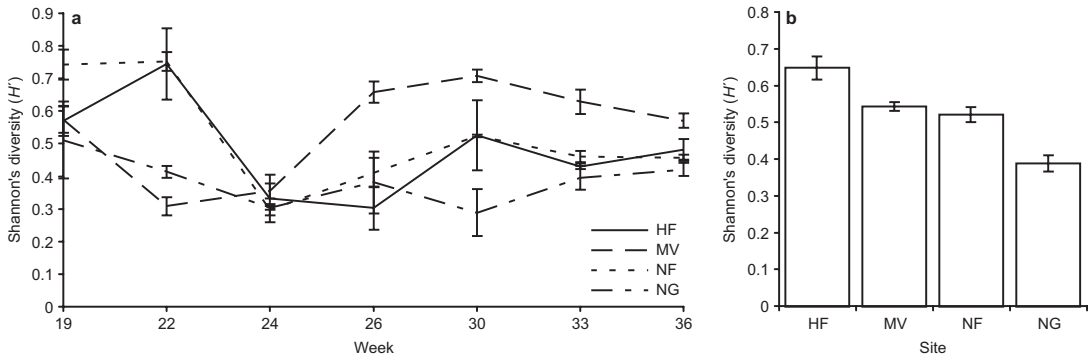


Fig. 7. (a) Shannon's diversity index values for the zooplankton communities (H') at the study sites during the survey season. (b) Average Shannon's diversity index values for zooplankton at the study sites (H'). HF = Hamnflada (mesotrophic), MV = Mjärdvik (eutrophic), NF = Norrflada (mesotrophic) and NG = Notgrund (eutrophic).

$p < 0.001$). The lowest average diversity, 0.38 ± 0.02 , was found in Notgrund. The value differed significantly (Tukey's HSD: $p < 0.001$) from the values for all the other sites.

Zooplankton β -diversity

Despite the low spatial variability in group richness, the assemblage of zooplankton communities differed substantially between the sites and along the season (Figs. 3 and 5). The percentage of groups in common for each pair of sites ranged from 48.0% to 62.5% (Table 3). The mesotrophic sites had more groups in common with each other than with the eutrophic sites. A similar pattern was typical to the eutrophic sites.

In contrast, Bray-Curtis similarity index values showed a distinct division into communities related to mesotrophic and eutrophic sites. The similarity values ranged from 9.7 to 13.7

between all pairs of sites representing different site types, whereas the values were 62.8 and 66.3 for the mesotrophic and the eutrophic pairs of sites, respectively.

Correlation analysis

Zooplankton abundance and biomass showed strong and significant correlations with the studied environmental parameters and with each other (Table 4). In contrast, group richness and Shannon's diversity index values could not be associated with any parameter in the survey. Strong, positive and significant correlations were found between zooplankton abundance and temperature ($R = 0.977$, $p = 0.023$), turbidity ($R = 0.954$, $p = 0.046$) and chlorophyll *a* concentration ($R = 0.996$, $p = 0.004$). Similar relationships between zooplankton biomass and total phosphorus concentration ($R = 0.994$, $p = 0.006$) and chlorophyll *a* concentration ($R = 0.958$, $p = 0.042$) were found.

Table 3. Bray-Curtis similarity index values (lower left) and percentages of groups in common (upper right) for each possible pair of survey sites. HF = Hamnflada (mesotrophic), MV = Mjärdvik (eutrophic), NF = Norrflada (mesotrophic) and NG = Notgrund (eutrophic).

		Groups in common			
		HF	MV	NF	NG
Bray-Curtis similarity index	HF	–	48.0%	62.5%	54.3%
	MV	9.8	–	52.3%	62.2%
	NF	62.8	9.7	–	48.8%
	NG	10.3	66.3	13.7	–

Discussion

Zooplankton quantity

As hypothesized, zooplankton abundance and biomass were significantly higher at the eutrophic than at the mesotrophic sites. The results are congruent with productivity-related patterns observed in temperate lakes (Scheffer 1998, Tallberg *et al.* 1999, Gyllström *et al.*

2005), and in coastal (Johansson 1992, Uitto *et al.* 1997) and open (Viitasalo 1994, Ojaveer *et al.* 1998) areas of the northern Baltic. Thus, productivity potential, largely determined by the concentration of total phosphorus and water temperature, appeared to control the quantity of zooplankton at the surveyed sites. Although ubiquitous, the differences between the site types became less prominent towards the end of the season. This shift took place concurrently with decreasing differences in the productivity-promoting factors — particularly temperature and the concentration of total phosphorus — followed by corresponding, levelled differences in chlorophyll *a* concentrations.

The major peaks in zooplankton abundance and biomass took place substantially earlier in the eutrophic than in the mesotrophic flads. Moreover, a secondary peak in zooplankton biomass appeared in Notgrund in mid-August. This was mainly attributable to mass occurrence of *Synchaeta* spp. The temporal patterns conflict with the ones reported from coastal (Johansson 1992, Viitasalo *et al.* 1995) and open (Viitasalo

1994) areas of the northern Baltic. Johansson (1992) reported a temporal shift in zooplankton biomass peaks in relation to increasing nutrient concentrations and decreasing salinity. Hence, compared with our results the order is opposite. Further, in the pelagic areas of the northern Baltic Sea the biomass peaks tend to occur between July and September (Johansson 1992, Viitasalo 1994, Uitto *et al.* 1997), that is, considerably later than at any of our survey sites. The study sites, in particular the ones with high productivity potential, rather resemble shallow temperate lakes with respect to the dynamics of zooplankton abundance and biomass (Scheffer 1998, Jeppesen *et al.* 2000). The early succession of the littoral zooplankton communities is most likely due to the rapid increase of water temperature and considerable detritus and nutrient runoff from land early in the spring. Such conditions favour production of planktic primary producers and detritivorous zooplankton directly which, in turn, constitute food for other zooplankton and thus benefit its production (Sobczak *et al.* 2005). The early zooplankton succession in littoral

Table 4. Pearson correlations (*r*) between four universal zooplankton community variables (D_{tot} = zooplankton abundance, BM_{tot} = zooplankton biomass, H' = Shannon's diversity index value, S = total number of zooplankton groups) and six environmental variables (P_{tot} = total phosphorus concentration, N_{tot} = total nitrogen concentration and $Chl-a$ = chlorophyll-*a* concentration). The calculations are based on whole-season average values for all variables.

Environmental variables		Zooplankton variables			
		D_{tot} (ind. l ⁻¹)	BM_{tot} (µg l ⁻¹)	$\log_{10}H'$	S
P_{tot} (µg l ⁻¹)	<i>r</i>	0.930	0.994	-0.852	0.293
	<i>p</i> (2-tailed)	0.070	0.006	0.148	0.707
	<i>n</i>	4	4	4	4
N_{tot} (µg l ⁻¹)	<i>r</i>	0.841	0.846	-0.803	0.387
	<i>p</i> (2-tailed)	0.159	0.154	0.197	0.613
	<i>n</i>	4	4	4	4
Salinity (psu)	<i>r</i>	-0.879	-0.853	0.734	-0.498
	<i>p</i> (2-tailed)	0.121	0.147	0.266	0.502
	<i>n</i>	4	4	4	4
Temp. (°C)	<i>r</i>	0.977	0.946	-0.550	0.607
	<i>p</i> (2-tailed)	0.023	0.054	0.450	0.393
	<i>n</i>	4	4	4	4
Turbidity (NTU)	<i>r</i>	0.954	0.912	-0.685	0.594
	<i>p</i> (2-tailed)	0.046	0.088	0.315	0.406
	<i>n</i>	4	4	4	4
$Chl-a$ (µg l ⁻¹)	<i>r</i>	0.996	0.958	-0.656	0.614
	<i>p</i> (2-tailed)	0.004	0.042	0.344	0.386
	<i>n</i>	4	4	4	4
Correlation is significant at the		0.01	0.05	level (2-tailed)	

areas has certainly profound effects at the next trophic level. Particularly the juveniles of virtually all fish species in the northern Baltic region depend on zooplankton as a food source at least during early developmental stages (Rogowski and Tesch 1960, Mehner and Thiel 1999 and references therein, Elliot and Hemingway 2002). Thus, the regional importance of littoral habitats can be regarded crucial for fish recruitment. However, it should be emphasized that also the species composition and size distribution of zooplankton communities are crucial for the impact of zooplankton on higher trophic levels (Brooks and Dodson 1965, Jeppesen *et al.* 2000).

Zooplankton diversity

In contrast to our hypothesis, the spatial variability of zooplankton diversity, as measured by the number of groups and Shannon's diversity index, was low. Thus, no distinction could be made between the mesotrophic and eutrophic site types, but the temporal variability was high. Similar seasonal dynamics was recorded for all sites. The number of zooplankton groups varied unimodally during the growing season, peaking around midsummer. Roughly reverse patterns were observed for Shannon's diversity index values, because the peaks in the number of zooplankton groups coincided with peaks in zooplankton abundance. In other words, the communities were dominated by few, abundant groups around midsummer. During this period, the mesotrophic sites were characterized by mass occurrence of *Synchaeta* spp., whilst the eutrophic ones were dominated by *Keratella quadrata* and *K. cochlearis*. By contrast, the zooplankton communities in all sites were more evenly represented by different groups in the beginning and the end of the survey season.

Both spatial and temporal differences in the assemblage of zooplankton communities were pronounced. The percentage of zooplankton groups in common was low for all the sites, especially for the mesotrophic and eutrophic types. Further, the turnover of zooplankton groups was rapid at all sites. Although some of the high spatial variability was attributed to groups occurring only occasionally and in

low abundances, clear differences in the community structure were found between the sites also in the similarity analysis compensating for such groups. Clearly the largest differences were found between the mesotrophic and eutrophic site types. Further, the seasonal dynamics of the groups generally dominating all the surveyed zooplankton communities differed considerably between the site types. For instance, the generally abundant *Keratella* species, *K. quadrata* and *K. cochlearis*, dominated the eutrophic sites in the beginning of the season, whereas the mesotrophic sites were characterized by ample occurrence of these species towards the end of the season. Further, the dynamics of copepod nauplii and juveniles provides another representative example on differences between the site types. These groups occurred abundantly at the mesotrophic sites in the beginning and in the end of the survey season. At the eutrophic sites, especially in the most eutrophic Notgrund, the relative abundance of copepod nauplii and juveniles exhibited almost reverse dynamics, peaking in the middle of the season.

A significant proportion of the zooplankton communities in the eutrophic sites consisted of *Keratella quadrata* and cyclopoid nauplii. The relative abundance of these small-bodied organisms was considerably lower in the mesotrophic sites. By contrast, large-bodied organisms, particularly different life stages of copepods, constituted a much higher proportion of the communities in the mesotrophic sites. These differences in the composition of zooplankton communities between the mesotrophic and eutrophic site types appeared to be the mainly attributable to differences in nutrient concentrations, salinity and temperature. Firstly, opportunistic rotifers and, consequently, adult and juvenile cyclopoids preying on them, tend to benefit from eutrophic conditions at least in lakes (e.g. Jeppesen *et al.* 2000). Thus, the increased fecundity of cyclopoids, facilitated by the rotifers as a food supply, can have contributed to the abundance of the cyclopoid nauplii in the eutrophic sites (Hansen and Santer 1995, Hopp *et al.* 1997). Moreover, the competitive advantage of calanoids over cyclopoids should increase in concert with decreasing planktic primary productivity, because the scarcity of food resources hinders

the development of cyclopoids more than that of calanoids. This, in turn, is expected to reduce the predation pressure on calanoid instars by the carnivorous cyclopoid stages (Santer 1994). Secondly, the comparably low abundance of copepods in the eutrophic sites may be explained by the fact that the proportion of copepods tends to decline (Vuorinen *et al.* 1998), whereas the relative abundance of cyclopoids inclines to increase (Dippner *et al.* 2001 and references therein) with decreasing salinity in the Baltic Sea. Thirdly, copepod development may be retarded by a fast rise of temperatures in the spring due to mismatching with food availability (Sommer *et al.* 2007). Thus, the mesotrophic sites were likely to be more favourable environments for copepods than the eutrophic ones.

The studied sites share the same pool of potential inhabitants and can thus be seen as parts of the same landscape. For the landscape level biodiversity of zooplankton in lakes, the most commonly observed relationship has been one of a unimodal peak in species richness at intermediate primary productivity (also often measured as lake trophic state or total phosphorus). In northern temperate lakes, primary productivity is strongly related to epilimnetic phytoplankton biomass (chlorophyll *a*), which in turn is tightly linked to total phosphorus levels (Barnett and Beisner 2007). Based on the high variability in productivity potential between the survey sites, we erroneously expected congruent differences in the diversity (group richness and Shannon's diversity index) of zooplankton.

However, our results need not indicate that productivity potential was not relevant in shaping the richness and diversity of zooplankton groups. The unimodal relationship has been suggested to be driven by diversity of food resources, spatiotemporal heterogeneity in food abundance (competitive interactions), habitat variability and/or predation intensity (Waide *et al.* 1999, Mittelbach *et al.* 2001). Although our survey did not directly address the actual driving mechanisms for biodiversity, some general points can still be considered. Firstly, the eutrophic sites were generally more fluctuating environments (Beisner 2001), i.e. the temporal variation in all the studied abiotic, environmental parameters was considerably higher in them than

in the mesotrophic sites. This variability probably also resulted in the higher temporal heterogeneity in the abundance of food (chlorophyll *a*) in the eutrophic sites. Unfortunately we have no estimates of the diversity of food resources in the sites. However, it is likely that the variability was high between the site types. At least in lakes, phytoplankton community composition varies strongly with productivity potential (Watson *et al.* 1997). Secondly, occurrence of zooplankton predators (small fish) has been shown to be an order of magnitude higher at the eutrophic than at the mesotrophic sites (Snickars *et al.* 2009). As for habitat variability, at least the complexity created by submerged macrophytes seems to vary with productivity potential in the study sites. Further, the assemblage of macrophyte communities differs significantly between the site types (K. Rosqvist unpubl. data). As no relationship between productivity potential and richness or diversity existed in our survey, the mesotrophic and eutrophic site types should (in theory) have been rather uniform with respect to the productivity-induced mechanisms determining zooplankton diversity. Such uniformity did not seem to hold true for the surveyed sites. Under the circumstances, the mechanisms seem to have been cancelled out by each other or an additional factor.

Previous studies suggest that the form of productivity–diversity relationship may be influenced by other abiotic, environmental factors (Mittelbach *et al.* 2001 and references therein). At the surveyed sites, salinity can function as such a factor. Even low variability in salinity can affect the species composition in brackish environments (Telesh and Heerkloss 2002, 2004, Persson and Schreiber 2004). Furthermore, the differences in salinity between the mesotrophic and eutrophic flads are likely to be more prominent during winter and early spring (Munsterhjelm 2005) — periods not included in the survey. These seasonal differences in salinity may have a significant effect on the early and more delicate developmental stages of different organisms as well as on the fecundity of their adult stages (e.g. Chinnery and Williams 2004). Thus, the potential effects of productivity potential on zooplankton group richness and diversity can have been ridden over by spatio-

temporal variations in salinity. In the Baltic estuaries species richness and diversity tend to have a unimodal relationship with salinity below a certain critical range (Remane 1934, Telesh 2004). This range is commonly between 5 and 8 psu in brackish waters (Cognetti and Maltagliati 2000). Gasiūnaitė (2000) observed highest species richness in a salinity range of 4.1–5.0 psu in a survey conducted in the Curonian Lagoon (Lithuania). In this area, the salinity levels vary somewhat equally with our study area. It is thus possible that the lower salinity levels at the eutrophic sites promoted higher diversity. At least the temporal variability in salinity was higher at these sites. Such variability has also been suggested as a boosting factor for species richness (Telesh 2004). Hence, the effects of salinity and productivity potential may have compensated for each other in our study sites. We suggest that this combination, the structural complexity (Meerhoff 2007) and the generally high temporal variability in environmental conditions (Hutchinson 1961) have led to the high α -diversity in the studied littoral zooplankton communities as compared with the surrounding open sea areas (Johansson 1992, Viitasalo 1994, Uitto *et al.* 1997, Ruokolainen *et al.* 2006). As for the observed high β -diversity, differences in productivity potential appear to be the ultimate explanation. Additionally, salinity seems to have a modifying effect on the composition of the zooplankton communities.

Conclusions

We conclude that temperature and total phosphorus appear to be the most potential regulating factors for shaping the littoral zooplankton communities in our study area. The abundance of zooplankton is clearly positively related to productivity potential, which, together with salinity, shapes the composition of the communities. However, productivity potential has no direct effect on the composition of zooplankton. Hence, in order to increase our understanding of the assemblage of communities, we emphasize further studies on the direct, biotic mechanisms behind the observed patterns. Future studies should at least stress how zooplankton commu-

nity structure is related to phytoplankton diversity, structural complexity and predation pressure.

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