Supervisors:

Docent Leena Nurminen  Docent Marko Reinikainen
Department of Environmental Sciences  Tvärminne Zoological Station
University of Helsinki, Finland  University of Helsinki, Finland

Docent Elina Leskinen  Professor Hannu Lehtonen
Department of Environmental Sciences  Department of Environmental Sciences
University of Helsinki, Finland  University of Helsinki, Finland

Advisory committee:

Docent Maiju Lehtiniemi  Docent Jaanika Blomster
Finnish Environment Institute  Department of Environmental Sciences
Helsinki, Finland  University of Helsinki, Finland

Reviewers:

Docent Maiju Lehtiniemi  Professor Mariana Meerhoff
Finnish Environment Institute  Faculty of Sciences
Helsinki, Finland  University of the Republic, Uruguay

Examiner:

Professor Jonathan Shurin
Section of Ecology, Behavior and Evolution
University of California- San Diego, USA

Custos:

Professor Jukka Horppila
Department of Environmental Sciences
University of Helsinki, Finland

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ABSTRACT

Zooplankton are considered an important link between the zooplanktivores that consume them and the lower trophic levels, yet their specific ecological role in littoral brackish ecosystems is still relatively unstudied. In general, ecological interest in zooplankton derives from their roles as grazers or as a food source. As grazers, their role is coupled with predicting future densities and composition of the algal community, while alternatively as prey they provide information on fish stocks in terms of the zooplankton production available to fish. This thesis aimed to unravel aspects related to these roles in the littoral zones of the Baltic Sea, by shedding light on the themes of zooplankton composition and diversity, the interactions between zooplankton and their predators, and the general feeding ecology of components of zooplankton.

The first objective of the thesis was to gain baseline information on zooplankton community composition and diversity in the littoral Baltic Sea via field sampling on a salinity gradient. The thesis also aimed to investigate how salinity and other abiotic factors, such as turbidity, temperature and wave exposure, affect zooplankton communities and the predation that structures them. Predation via two types of feeding by zooplanktivorous fish was studied experimentally as a regulator of zooplankton communities. Finally, the thesis investigated the role of copepod nauplii as grazers in laboratory conditions.

Salinity was found to be the most significant abiotic driver of spatial patterns of composition and diversity of zooplankton. Turbidity/chl a also influenced community structure to a lesser extent. The spatial patterns of species heterogeneity remained relatively constant regardless of temporal turnover, and there was an abrupt change in species composition at an intermediate salinity of 4 (on the Practical Salinity Scale) on the salinity gradient. Functional diversity of zooplankton was found to be related to salinity, but also to factors related to productivity after a certain threshold. Zooplankton diversity was also affected by predation, but this effect was regulated by the initial composition of the zooplankton community, which was in turn directly related to seasonality. Predation itself was found to structure the community through direct removal of crustacean zooplankton, as well as cascading effects on microzooplankton. These effects, as well as the extent of the disturbance generated by turbidity on zooplanktivorous feeding, were all closely related to predator type.

In the final section of the thesis, which concentrated on zooplankton as consumers, the functional responses of stage NII nauplii of the calanoid copepod *Paracartia grani* to various microalgae were found to be either Holling type II or III responses. Highest maximum clearance rates were found on a diatom and a dinoflagellate of a
size of ~12 µm, indicating an optimal prey:predator size ratio of 0.08. In plurialgal mixtures, feeding patterns were largely dependent on prey type.

Zooplankton are irrevocably linked to phytoplankton and fish through food web interactions. Changes in the abiotic environment inevitably lead to a response in the biotic environment as well, and a bottom-up resource level response reflects on top predators, in this case the littoral fish. Therefore, understanding the abiotic and biotic factors determining zooplankton diversity and density is a precondition to understanding the links between phytoplankton, zooplankton, and coastal zooplanktivores.
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I  Helenius LK, Lehtonen H, Leskinen E & Nurminen L. Spatial patterns of littoral zooplankton assemblages along a salinity gradient in a brackish sea: a functional diversity perspective. *(Submitted manuscript)*


IV Helenius LK & Saiz E. Feeding ecology of early stage nauplii of the calanoid copepod Paracartia grani: feeding rates, prey size spectrum and selectivity. *(Manuscript)*

Data not included in publications are presented in addition.

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## AUTHOR CONTRIBUTION

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LH – Laura Helenius a), b)  
AAP – Anna Aymà Padrós c), d)  
EL – Elina Leskinen a)  
ES – Enric Saiz c)  
HL – Hannu Lehtonen a)  
JB – Janica Borg c)  
LN – Leena Nurminen a)  

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a) Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland  
b) Tvärminne Zoological Station, University of Helsinki, J. A. Palménin tie 260, 10900 Hanko, Finland  
c) Institute of Marine Sciences, (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain  
d) GRC Marine Geosciences, Department of Marine Stratigraphy, Paleontology and Geosciences, University of Barcelona, Carrer Martí i Franquès s/n, 08028 Barcelona, Spain  
e) Helcom Secretariat, Baltic Marine Environment Protection Commission, Katajanokanlaituri 6B, FI-00160 Helsinki, Finland
**ABBREVIATIONS**

<table>
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<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>ANOSIM</td>
<td>Analysis of similarities</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>Chl a</td>
<td>Chlorophyll a (proxy for algal biomass)</td>
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<tr>
<td>DistLM</td>
<td>Distance based linear modelling</td>
</tr>
<tr>
<td>ESD</td>
<td>Equivalent spherical diameter</td>
</tr>
<tr>
<td>FD</td>
<td>Functional diversity</td>
</tr>
<tr>
<td>$F_{max}$</td>
<td>Maximum clearance rate</td>
</tr>
<tr>
<td>FSW</td>
<td>Filtered seawater</td>
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<td>GAM</td>
<td>Generalized additive model</td>
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<tr>
<td>$H'$</td>
<td>Shannon-Weaver diversity index</td>
</tr>
<tr>
<td>ICM</td>
<td>Institut de Ciències del Mar</td>
</tr>
<tr>
<td>$I_{max}$</td>
<td>Maximum ingestion rate</td>
</tr>
<tr>
<td>$K_m$</td>
<td>Half-saturation food concentration</td>
</tr>
<tr>
<td>$K_t$</td>
<td>Food concentration at $F_{max}$</td>
</tr>
<tr>
<td>MWS</td>
<td>Mean weighted size</td>
</tr>
<tr>
<td>nMDS</td>
<td>Non-metric multidimensional scaling</td>
</tr>
<tr>
<td>NTU</td>
<td>Nephelometric turbidity units</td>
</tr>
<tr>
<td>PCA</td>
<td>Principal component analysis</td>
</tr>
<tr>
<td>PCO</td>
<td>Principal coordinate ordination</td>
</tr>
<tr>
<td>PERMANOVA</td>
<td>Permutational multivariate ANOVA</td>
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<tr>
<td>PSS</td>
<td>Practical Salinity Scale</td>
</tr>
<tr>
<td>RMA</td>
<td>Repeated measures ANOVA</td>
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<tr>
<td>SIMPER</td>
<td>Similarity percentages procedure</td>
</tr>
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<td>SIMPROF</td>
<td>Similarity profile</td>
</tr>
<tr>
<td>TN</td>
<td>Total nitrogen</td>
</tr>
<tr>
<td>TP</td>
<td>Total phosphorus</td>
</tr>
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<td>TZS</td>
<td>Tvärminne Zoological Station</td>
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1 INTRODUCTION

1.1 THE LINK BETWEEN FOOD WEBS AND DIVERSITY

Food webs are essentially networks which record the dynamic interactions, or simply the flow of energy and resources, between species or functional groups inside ecosystems. The basic architectural characteristics of a food web depend on its connectance (the proportion of possible links that are realized), how the links are distributed, and the interaction strengths between species (Winemiller & Layman 2005). Recent studies indicate that most food webs are rife with omnivory, and interspecies links are mostly inactive at any specific point in time, due to a high proportion of generalist predators (Dunne et al. 2004). This complexity increases with species richness and level of connectance, and in turn, both species richness (Tilman et al. 1996; McGrady-Steed et al. 1997; Naeem & Li 1997; Cardinale et al. 2002) as well as species composition contribute to biodiversity–ecosystem functioning relationships (Hooper & Vitousek 1997; Symstad et al. 1998). It follows that food webs and species diversity are highly linked concepts, and many central studies in aquatic ecology deal with the relationship between the two, as diversity in the form of relative species abundance ultimately determines functional responses, adaptive foraging and prey switching in food webs (e.g. Paine 1966; Leibold 1996; Worm et al. 2002).

Biodiversity can be defined, in its simplest form, as the way the total biomass of a community or assemblage is partitioned among species. Species diversity is regulated by variation in the intensity of predation, competition and/or disturbance (Paine 1966; Connell 1978). Species richness is often used as a measure of diversity, but in fact the functional characteristics and ecological roles of organisms, rather than their taxonomic identity, may be more relevant in examining effects on ecosystem level processes (Walker 1991; Hooper & Vitousek 1997; Walker et al. 1999; Symstad et al. 2000). Functional diversity is therefore based on the functional traits of all the species in a community. The functional classification of organisms has become more common in studies on biodiversity-ecosystem functioning relationships in terrestrial (e.g. Walker & Langridge 2002) and aquatic systems (e.g. Bady et al. 2005). In determining functional groups, traits can be defined by the specific process of interest, such as resource use in the case of zooplankton grazing (e.g. Barnett et al. 2007). Functional traits also describe how species may respond to the environment and perturbations in it, and knowing the traits present in a community increases the power of models that predict how a community will shift in the incident of environmental change (Norberg 2004).
1.2 THE BALTIC SEA AS A STUDY SYSTEM: ZOOPLANKTON AND BEYOND

The Baltic Sea is a shallow but large brackish sea, characterized by a temporally stable salinity gradient, reaching from $> 20$ on the Practical Salinity Scale (PSS) in the opening area towards the North Sea to approximately 2 in the Bothnian Bay (Kullenberg 1981). The fauna and flora are of both marine and freshwater origin, in addition to brackish water species, and their large-scale distribution is directly related to the existing salinity gradient (Hälfors et al. 1981; Snoeijis 1999). Due to the fact that both marine and freshwater species live at their physiological limits in the Baltic Sea, it supports fewer species than true marine or freshwater areas generally do, and therefore its food webs are less complex (Elmgren 1984; Ojaveer et al. 2010). Because of its young age and recent rapid evolution from limnic to fully marine to brackish conditions, as well as the ongoing niche occupation illustrated by the numerous species invasions, the Baltic Sea is also characterized by high instability and variability of both abiotic and biotic conditions (Menge & Sutherland 1987; Alenius et al. 1998). The field sampling area of this thesis is located in the Gulf of Finland in the northeastern corner of the Baltic, where there is a permanent halocline caused by the continuous freshwater discharge from rivers and the irregular saline pulses from the North Sea (Kullenberg 1981). This limited water exchange with the North Sea, combined with a large catchment area, inevitably leaves the Baltic Sea generally vulnerable to a variety of human activities, including maritime shipping, fisheries and nutrient supply via riverine runoff (HELCOM 2009). In particular, the coastal areas in the Gulf of Finland suffer from increasing eutrophication caused by excessive nutrient release, and subsequently, the resulting turbidity and deterioration of visual and light conditions in the water column (Cederwall & Elmgren 1990; Pitkänen et al. 2001; Schiewer 2008).

Mesozooplankton communities are generally dominated by copepods in marine areas, while cladocerans are considered a primarily freshwater group (Rudstam et al. 1994; Forró et al. 2008). The unique brackish elements of the Baltic Sea render the zooplankton community in this area an intriguing mixture of both marine and freshwater species (Koski et al. 1999a). Historically, the overall diversity of zooplankton in the Baltic Sea has been presumed to be decidedly low (e.g. Ackefors 1981). The general consensus has been that the variable environmental conditions and resulting instability of estuaries and other transitional aquatic areas limits species occurrence, and results in species-poor communities in brackish areas (McLusky & Elliott 2004). The Artenminimum (‘species minimum’) concept of Remane (1934) stated that taxonomic diversity is at its lowest at the horohalinicum, at a salinity of 5 – 8. However, the notion of low zooplankton diversity has recently been challenged as outdated, having resulted purely from previous underestimation of microzooplanktonic species and general limitations in
taxonomic knowledge (Ojaveer et al. 2010; Telesh et al. 2011). Nearly 400 species of planktonic ciliates, rotifers and crustaceans are currently known from estuarine and coastal ecosystems of the Baltic Sea, with the most species-rich component being microzooplankton (ciliates and rotifers) (Telesh & Heerkloss 2002; 2004). Of ciliates, the aloricate oligotrichs (e.g. genera *Strombidium*, *Strobilidium* and *Lohmaniella*) and the tintinnids are abundant (Garstecki et al. 2000), while rotifers of the families Synchaetidae and Brachionidae contribute to total zooplankton biomass throughout the Baltic Sea (Witek 1995; Telesh & Heerkloss 2002). Up to 95% of zooplankton biomass in Baltic coastal ecosystems is made up of rotifers, but their influence in terms of diversity and abundance decreases with increasing water salinity (Telesh 2004). Excluding rotifers, which are often included as mesozooplankton in Baltic Sea monitoring data, the dominant coastal mesozooplankton in the Gulf of Finland are the calanoid copepod genera *Acartia* and *Eurytemora*, some species of which tolerate wide salinity ranges (Ojaveer et al. 2010). Accordingly, these two copepod genera and their interactions feature in much of the literature on zooplankton distribution and food web processes in the northern Baltic Sea (e.g. Hansson et al. 1990; Viitasalo et al. 1994; Engström et al. 2000; Viitasalo et al. 2001; Sopanen et al. 2006). Neritic cladocerans in the general area include podonids (genera *Podon*, *Evadne*) and bosminids (*Eubosmina*) (Ojaveer et al. 1998; Vuorinen et al. 1998).

Because monitoring of coastal plankton is generally conducted in areas with vertical depths of over 20 meters, the studies characterizing zooplankton distribution and ecology in the Baltic Sea have been conducted in adequately deep coastal waters or further pelagic areas (e.g. Viitasalo et al. 1995; Uitto et al. 1997; Vuorinen et al. 1998; Koski et al. 1999a; Telesh 2004). Until recent attention on their diversity and dynamics (e.g. Scheinin & Mattila 2010), littoral zooplankton communities of shallow Baltic Sea waters (< 2 m depth) have remained relatively unstudied, despite the strong interaction potential between zooplankton and fish juveniles and larvae in these shallow zones.

Zooplanktivorous fish in the littoral zones of the Baltic Sea consist of juvenile cyprinids and percids, and small, commercially unimportant species of both freshwater and marine origin (Rajasilta et al. 1999). The three-spined stickleback (*Gasterosteus aculeatus* L.) is a small euryhaline fish, and the most common littoral fish species in the northern Baltic Sea (Lemmetyinen & Mankki 1975; Rajasilta et al. 1999; Ljunggren et al. 2010). The stickleback has been established as a central link in the Baltic Sea food web, and a key consumer of zooplankton (Lemmetyinen & Mankki 1975; Peltonen et al. 2004). Increases in stickleback populations and other mesopredatory fish in the Baltic Sea have been credited to the fishery-induced decrease in offshore piscivorous predators, combined with the continuous decline in the densities of dominant nearshore predators such
as European perch (*Perca fluviatilis*) and northern pike (*Esox lucius*), which have generated a mesopredator release in coastal areas (Eriksson et al. 2011). An increase in mesopredatory fish has been associated with community-wide cascading effects on lower trophic levels, including shifts in plankton biomass (e.g. Casini et al. 2008; Eriksson et al. 2009; Sieben et al. 2011).

1.3 THE IMPORTANCE OF ZOOPLANKTON: ASPECTS OF COMPOSITION AND DISTRIBUTION

Zooplanktivores utilize a range of feeding strategies, which reflect on their physical capacities and target prey. The stickleback is a vision-oriented selective particulate feeder, which seeks out and attacks individual prey items (Wootton 1984; Lazzaro 1987). An alternate, non-selective filter-feeding strategy is used by cyprinids, such as the roach (*Rutilus rutilus* L.), which is an efficient particulate feeder in clear water but may switch to filter feeding to maximize prey intake in compromised visibility (Lammens et al. 1987; Diehl 1988). The roach is also common in littoral zones of the Baltic Sea, and stocks have increased considerably in the last 20 years, with trends similar to other cyprinid fish stocks (Lappalainen et al. 2001; Lehtonen & Rask 2004). The roach population increase is largely attributed to coastal eutrophication, which causes low visibility conditions that favor filter-feeding strategies (Lappalainen et al. 2001; Nurminen et al. 2010). Because of their ecological parallels and potential resource competition, as well as the increasing strength of the trophic presence of the roach due to environmental conditions, these two key zooplanktivores and the effect of their differing feeding strategies on littoral zooplankton communities are of central interest in this thesis.

Zooplankton can be considered a significant trophic link between primary producers and higher consumers, and therefore they play a major role in aquatic food webs. As a grazing component, they can shape phytoplankton communities, and limit or enhance productivity (Redfield 1980; Sterner 1989; Brett et al. 1994; Jeppesen et al. 1990; Sommer et al. 2001; Muylaert et al. 2006). As mediators of energy to higher trophic levels they are a significant prey item for invertebrates (Albertsson & Leonardson 2001; Viherluoto & Viitasalo 2001) and fish and their larvae (Turner 1984; Gliwicz & Pijanowska 1989; Mehner & Thiel 1999; Elliott & Hemingway 2002). Zooplankton species differ in their nutritional content and their importance as prey items, and substantial changes in zooplankton composition can quickly reflect on their predators (e.g. Vuori & Nikinmaa 2007). Because of their position as intermediaries in the food web, zooplankton are fundamentally involved in a multitude of ecosystem processes, and understanding the distribution and composition of zooplankton communities in a system is paramount to unraveling the mechanisms that shape abiotic and biotic processes in that system.
Traditional niche-based theory assumes that deterministic factors, including species traits, interspecies interactions and environmental conditions, control local community composition (Chesson 2000). In theory, the resulting local communities then should have little variation in species composition between sites (i.e. exhibit low β-diversity) if the environmental conditions are similar, and random stochastic factors discounted (Chase et al. 2009). Community composition of organisms is then generally shaped by both internal processes, such as predation and competition, as well as external processes related to the environment (Menge & Olson 1990). The surrounding physical environment acts as a physiological filter, by limiting species distribution according to tolerance limits (Remmert 1983). Environmental conditions have a primary role in shaping species patterns, and their fluctuations can both facilitate as well as exclude species, through turnover or migration (Hillebrand & Shurin 2005; Shurin et al. 2010).

In marine coastal areas, some of the main environmental parameters that can affect community composition of organisms are salinity, wave exposure and temperature (Magill & Sayer 2002; Bonsdorff et al. 2003; Boström et al. 2006). In addition, aquatic environments with steep horizontal gradients of salinity and nutrients, such as the Baltic Sea, usually support communities that are generally controlled by interactions between abiotic and biotic characteristics, as well as meteorological conditions (Li et al. 2000; Froneman 2001; 2004; Telesh 2004). The characteristically spatially and temporally heterogeneous conditions in these environments can produce significant spatial variability in the distribution of species, whereas extreme and/or long-term variations in salinity can define the species richness of associated communities (de Jonge 1974; Michaelis et al. 1992; Li et al. 2006). Indeed, in terms of zooplankton specifically, salinity, water temperature and active chl a are considered crucial factors in controlling their distribution in brackish and estuarine conditions (Gaughan & Potter 1995; Viitasalo et al. 1995; Froneman 2001; 2004).

While species-specific tolerances to physical parameters determine the species that have the potential to occur in a habitat, biotic interactions can determine the actual community composition. Negative interactions, through competition or predation, can restrict the distribution of a species (Black & Hairston 1988; Brooks & Dodson 1965) or limit its population density (Thorp 1986). Therefore, the relative strengths of the biotic interactions, in the setting of the physical constraints, shape community structure on an environmental gradient.

1.4 ZOOPLANKTON AS PREY: PREDATION AND ITS EFFECTS

Predation is defined as a series of discrete events occurring between predator and prey: the location of prey, followed by pursuit, attack, capture, handling and ingestion (Holling 1959; O’Brien...
In predator-prey interactions, the intake rate of an individual predator is determined by attack rate and handling time (Holling 1959). Inevitably, the effects of predation depend on predator efficiency, and ultimately can vary and change with environmental conditions, which can influence either of these components (O’Brien 1987). For example, aquatic predators that use visual cues are highly influenced by the light level and clarity of the surrounding water, and accordingly, elevated turbidity has been found to be deleterious to the feeding of vision-oriented fish (Vinyard & O’Brien 1976; Gardner 1981; Hayes & Rutledge 1991; Benfield & Minello 1996; Rowe & Dean 1998; Nurminen & Horppila 2006).

Prey selection is another aspect of predation that can potentially be influenced by environmental conditions and feeding strategy. The rates, durations and efficiencies of the components of the predation process, as well as their dependencies on food availability, define the functional response (Holling 1959). A key concept in theories on predator-prey interaction is the functional response, which defines the relationship between prey density and predator consumption rate (Solomon 1949; Holling 1959). Conventionally, three functional response types are described, deemed Holling type I (a linear increase in ingestion rate as a function of prey density), type II (curvilinear decelerating increase), and type III (sigmoidal increase) responses (Holling 1959) (Fig. 1a). Yet for any specific predator, parameters related to the functional response vary for different prey types, implying that prey are ingested at different rates, and therefore, feeding is selective. Selective feeding is directly related to prey switching, as predators are known to alter their prey choice in the face of changing prey abundance (e.g. Oaten & Murdoch 1975). Prey selection and switching play an important role in maximizing foraging success in aquatic predators, and disparate feeding strategies have been shown to target different prey species (Reiriz et al. 1998; Estlander et al. 2010). Yet in the incidence of an environmental change, there may be a shift in the type of prey captured (Rowe 1984; Gregory & Northcoate 1993; Salonen & Engström-Öst 2010) or an impediment to size selective feeding (Rowe et al. 2003).

In terms of zooplanktivory, plankton body size correlates with susceptibility to predation by fish, and hence prey species differ in their vulnerability to predation (Brooks & Dodson 1965). Attack rates of fish are also generally higher on slow cladocerans than fast and evasive copepods, resulting in an increased intake of the former prey type in relation to the latter (Drenner et al. 1978; Persson 1987a). In zooplankton communities, prey selection generally results in the direct depletion of selected crustacean prey, and the effects can cascade through other non-target zooplankton species, and on through phytoplankton to influence ecosystem processes (Carpenter et al. 1985; Chang et al. 2004; Hansson et al. 2007).
Strong community-wide predation effects, such as trophic cascades, are presumed to be especially common in aquatic ecosystems (Carpenter et al. 1985; Strong 1992; Shurin et al. 2002). Predators are able to control prey populations by changing their relative and absolute abundances, species composition and population structure (Carpenter et al. 1985; Hansson et al. 1990; Uitto et al. 1995), but also species beyond their target prey by releasing the prey population of their target prey from predation pressure (Carpenter et al. 1996). For example, zooplanktivorous predators have the potential to increase primary productivity by simply reducing the amount of herbivorous zooplankton (Brett & Goldman 1996; Shurin et al. 2002). Therefore, predation by zooplanktivores is considered a major driving force in shaping plankton communities, and hence a determinant of their structure (Holt 1984; Sommer et al. 1986).
The plankton ecology group (PEG) model (Sommer et al. 1986) has been used to explain patterns in the seasonal succession of zooplankton in marine as well as freshwater systems. It describes the biotic interactions which unfold over a growing season, including species replacement. The unequivocal role of fish predation in structuring zooplankton communities by the size-selective removal of mesozooplankton is emphasized in the PEG model. It has been suggested, that predation by fish has the potential to drive zooplankton succession in some aquatic systems (Cryer et al. 1986; Gliwicz & Pijanowska 1989), and recent data emphasize the importance of predation in shaping zooplankton communities (Hansson et al. 2007). With sufficiently high predation pressure, zooplankton populations can even collapse irrespective of resource availability (Nicolle et al. 2011). Nonetheless, the complete removal of prey species, resulting in local extinction and hence reduction of total prey diversity, is not the imminent consequence of all predation.

In general, the effects of predators on prey diversity come across via two conflicting mechanisms: 1) predators either reduce prey biomass by increasing prey mortality or reducing prey reproduction, or alternatively 2) predators prevent competitive exclusion of prey species and apparent competition, and thus maintain diversity (Hillebrand & Shurin 2005). In the latter case, predators can generate resources, increase resource diversity or add limiting factors, therefore promoting the coexistence of competing prey. Even in a single study system, they can have positive or negative effects on community diversity, depending on circumstances related to either the predator-prey interaction itself or to the abiotic/biotic factors in the surrounding habitat (Shurin 2001; Hillebrand 2003). For example, the degree of prey dispersal can determine whether predators decrease prey community diversity significantly or not (Shurin 2001).

Predation can have a major impact on interspecific competitive interactions, and the extent of the impact depends on factors such as the scale of measurement (individual vs. population), the intensity of predation and the degree of prey selectivity (reviewed by Chase et al. 2002). Selective predation on dominant competitors can increase prey diversity when the other competitors are capable of coexistence: Predators promote prey diversity when they consume dominant prey species, and actively selecting predators potentially switch to consuming the most abundant prey, acting as a stabilizing factor in maintaining prey diversity (Chesson 2002; Kondoh 2003). Therefore, different predators with distinct feeding strategies are expected to have different effects on the composition and diversity of their prey communities, depending on the degree of selectivity and adaptive foraging switches of the predator.
1.5 ZOOPLANKTON AS CONSUMERS

Zooplankton are important prey to higher trophic levels, but also act as grazers, as well as predators of other zooplankton. In aquatic food webs, zooplankton biomass is not always directly derived from that of phytoplankton, because the quality and availability of phytoplankton as a food source differs according to species (Ahlgren et al. 1990; Sterner et al. 1993). Phytoplankton can affect its consumers through several different factors: i) the size and shape of the food particles, food selectivity and ingestion rates, ii) possible morphological defences against digestion, iii) nutritional paucity in terms of P, N and fatty acids, and/or iv) toxicity (reviewed by Gulati & DeMott 1997). Survival, growth and egg production of zooplankton can be severely weakened by low-quality or toxic phytoplankton (Uye 1996; Turner & Tester 1997; Koski et al. 1999b; Sopanen et al. 2006), thereby limiting the biomass of zooplankton prey available to higher trophic levels. Phytoplankton nutritional quality is not a straightforward concept, but can be defined by its content of highly unsaturated fatty acids (HUFAs), which are essential in survival, growth and reproduction of marine and freshwater zooplankton (Brett & Müller-Navarra 1997). Zooplanktivorous fish in turn depend on zooplankton for HUFAs, which are also important to their growth (Desvilettes et al. 1997) and larval development (Sargent et al. 1995). Hence the amount of energy and essential fatty acids that are transferred from zooplankton to higher trophic levels are dictated by the types and amounts of phytoplankton consumed by grazers.

In terms of zooplankton feeding on algae, the functional response can also be plotted as clearance rate (volume swept clear individual\(^{-1}\) time\(^{-1}\)) as a function of prey density (Fig. 1b). This allows for better separation between type II and type III responses, which can appear similar at high prey densities. Increasing the predictive power of aquatic food web models requires detailed knowledge of such prey-specific functional responses of organisms. In shallow littoral habitats, grazing zooplankton even have the potential to regulate regime shifts in terms of macrophyte and phytoplankton domination (Jeppesen et al. 1998; Scheffer 1998; Perrow et al. 1999). Consequently, in the case of zooplankton, details on these responses are crucial, particularly when attempting to predict the outcome of grazing control of algae in eutrophic systems, such as the Baltic Sea (Fussman & Blasius 2005).

Zooplankton functional responses have been investigated and quantified for a large array of copepods (Lampitt & Gamble 1982; Krylov 1988; Kiørboe et al. 1996; Saage et al. 2009; Zamora-Terol & Saiz 2013), cladocerans (Horton et al. 1979; Porter et al. 1983; Chow-Fraser & Spules 1992) and rotifers (Iyer & Rao 1996; Mohr & Adrian 2000). Larval stages of planktonic crustaceans are less studied. Yet nauplii of copepods, for example, make up large proportions of copepod biomasses in nature and therefore presumably have a high impact on grazing processes (Fryer 1986;
Castellani et al. 2007), as well as act as a major food source for fish larvae (e.g. Dalpadado et al. 2000; Gaard & Reinert 2002). Notably, nauplii of the calanoid copepod family Acartiidae are widespread and often numerically dominant in coastal areas around the globe, as the group prevails in a multitude of salinity conditions and has a high degree of tolerance for environmental change (Mauchline 1998).

Food type and availability are some of the major factors driving copepod feeding in natural systems (Saiz & Calbet 2011). It has long been known that zooplankton in general respond differently to potential food items (Gliwicz 1970). Additionally, the rate of intake of one prey type may be affected by the presence of alternative prey choices. Copepods are known to be size-selective omnivores, feeding on protozoans and large phytoplankton (Katechakis et al. 2002; Kleppel 1993; Sell et al. 2001; Sommer & Stibor 2002), and they have been shown to actively select or reject food particles (Paffenhöfer et al. 1982; Schultz & Kiørboe 2009). Complex feeding behaviors have been described for copepods, in which selection depends not only on size, but on the interplay between cell size and abundance (e.g. Wilson 1973; Kiørboe et al. 1996). Yet relatively little is known about the feeding rates and selectivity of naupliar stages. Even though early experimental work on nauplii feeding selectivity was conducted by Fernández (1979), empirical observations on feeding in controlled plurialgal suspensions are still scarce.
2. THESIS OBJECTIVES

Gaps remain in the knowledge surrounding coastal zooplankton distribution, diversity and interactions with other trophic levels. The main objective of this thesis was to present a comprehensive account of the composition, distribution, and diversity of littoral zooplankton communities in the Baltic Sea, and to examine their role as prey and consumers in the surrounding ecosystem (Fig. 2). This thesis is composed of four studies (numbered I – IV), which discuss the following themes with their respective specific aims:

I. What abiotic factors determine zooplankton distribution and diversity in the littoral Baltic Sea?

II. How does increasing turbidity affect the efficiency and selectivity of zooplanktivory by two littoral predators with varying feeding strategies?

III. How do these two zooplanktivores shape the diversity and dynamics of littoral zooplankton communities?

IV. How do the functional responses of a common copepod nauplius to different microalgal prey types vary?

Fig 2. A conceptual model of components of the littoral food web and the main questions of the thesis. Red arrows indicate conceptual effect links, black arrows indicate trophic links.
1) Zooplankton diversity and distribution: To give a detailed description of the species composition and structure of littoral zooplankton communities, including fractions of the often overlooked microzooplankton component, in a representative area of the northern Baltic Sea. To examine spatial patterns and diversity of the community over a subtle coastal salinity gradient, and investigate locally variable environmental factors (temperature, wave exposure, degree of eutrophication) as possible drivers of spatial heterogeneity in diversity and species occurrence (I).

2) Zooplankton as prey and zooplanktivory as a process: To examine the influence of environmental change, in the form of increasing turbidity, on predation by zooplanktivorous fish with different feeding strategies. In effect, to determine whether zooplankton prey types have different vulnerabilities to selective predation under turbid conditions (II). Moreover, to examine the effects of predation by the same zooplanktivores on the structure and diversity of littoral zooplankton communities, and to compare the extent to which top-down control by the different predators mediates varying responses in interactions within their prey communities (III).

3) Zooplankton as consumers: To experimentally investigate the feeding ecology of a larval life stage of a ubiquitous calanoid copepod (Paracartia grani Sars), and determine its prey size spectrum and functional responses to different microalgal prey types (IV).
3 MATERIALS AND METHODS

3.1 STUDY AREA AND FIELD SAMPLING (I)

The Gulf of Finland is a eutrophic, highly seasonal sub-estuary of the Baltic Sea. The fragmented Tvärmnne Archipelago in Hanko, Finland, is a well-studied area, where the Tvärmnne Zoological Station (University of Helsinki; hereafter referred to as TZS) is located. Sampling took place at 31 shallow coastal bays along a 40 km salinity and exposure gradient from the outer archipelago to just outside the semi-enclosed fjord-like Pojo Bay in the north (Fig. 3). The Pojo Bay is separated from the outer archipelago by a 7 m deep sill that prevents the renewal of deep water in the bay, and there is a high inflow of freshwater from the Mustionjoki River at the north end of the bay. Saline Baltic water moves landward periodically from the open sea. Primary production in the archipelago and the open sea areas is mainly limited by the availability of nitrogen (Kivi et al. 1993), and in the bay area by that of phosphorus (Lignell et al. 1992). Similar to other shores of the northern Baltic Proper, the coast is divided into zones, which are characterized by distinct morphological, hydrographical and biological features: a Pojo Bay zone, a mainland zone, inner and outer archipelago zones and an open-sea zone (Halme 1944; Niemi 1973; Munsterhjelm 2005), representing an estuarine salinity surface water gradient of 2 – 7. According to these traditional zonation classes of the Tvärmnne Archipelago, the sampling sites in study I geographically belonged to either the outer archipelago zone (hereafter referred to as OZ, sites 1 – 18), the inner archipelago zone (IZ, sites 19 – 25) or the mainland zone (MZ, sites 26 – 31). Salinity measured on the sampling gradient ranged from 6 to 2.6 from the outer archipelago to the mainland zone, respectively, with consistently higher salinities recorded later in the summer season.

The sites represented shallow beaches with a fine, sandy bottom substrate, and were sampled in June/July 2009 and in August in 2010, outside of rotifer abundance peaks estimated from previous sampling in the area. Sampling was conducted in the near vicinity of the shore at a depth of 0.8 – 1.2 meters. Zooplankton samples were collected with 1 meter horizontal hauls using a modified plankton net with a buoy, with a mesh size of 25 µm, and with 0.8 – 1 meter vertical hauls using a standard plankton net with a mesh size of 50 µm. The water volume filtered was estimated (without a flowmeter) as approximately 13 L and 40.2 L for the horizontal and vertical tows respectively. Samples were immediately fixed with 5% acid Lugol’s solution. Water samples were taken for measurements of nutrients, algal biomass, salinity and turbidity. Other environmental variables measured included temperature and wave exposure. Estimations of wave exposure were made according to the Baardseth index, which resulted in a value between 0 (indicating absolute shelter) and 40 (indicating maximal exposure) (Baardseth 1970).
Macrophyte coverage at each site was estimated by diving in 2009. In 2010 all environmental variables were additionally recorded with a YSI-6600 sonde (YSI Corp.).

3.2 EXPERIMENTAL WORK (II, III, IV)

Experimental work consisted of aquarium experiments, *in situ* mesocosm experiments, and laboratory feeding experiments. Aquarium and mesocosm experiments were conducted at TZS, while copepod nauplii feeding experiments were conducted at the Institut de Ciències del Mar (ICM, Barcelona, Spain).

3.2.1 EXPERIMENTAL FISH AND ZOOPLANKTON

Two common brackish water littoral zooplanktivorous fish of a similar size but with varying feeding strategies were used for experimental work concerning predation on zooplankton (II, III): the vision-oriented particulate feeding three-spined stickleback (*Gasterosteus aculeatus* L.) and the filter feeding juvenile roach (*Rutilus rutilus* L.). All fish were caught with a beach seine from the vicinity of the TZS and kept in aerated housing tanks at a temperature of 18 – 19°C and an indoor 16:8 light:dark regime. For the aquarium experiments (II) fish were acclimated in their experimental tanks in the respective experimental turbidity conditions for at least 12 hours before being used for experiments.

Zooplankton for the aquarium and mesocosm experiments (II, III) were collected from the vicinity of the TZS from depths of 1.5 to 15 meters using plankton nets of 100 to 200 µm mesh size. Prey items for use in the aquarium experiments, including two genera of copepods (*Acartia* and *Eurytemora*) and a cladoceran species (*Daphnia longispina*), were individually picked into FSW using pipettes.

For the nauplii feeding experiments (IV), the naupliar stages of the calanoid copepod *Paracartia grani* Sars were obtained from the continuous culture of the ICM. Copepods were grown in 20 L methacrylate cylinders at 18°C with a 12:12 light:dark cycle and fed with the cryptophyte *Rhodomonas salina*. Cohorts of stage NII nauplii were obtained by first collecting eggs using a vacuuming procedure with several filters to separate eggs from copepods. After cleaning with FSW, approximately 500,000 eggs were transferred to a new cylinder to hatch and grow in a suspension of *R. salina*. Eggs that were unhatched after 24 hours were cleaned out of the cylinder. 50 hours after the original egg collection the nauplii were determined to be at the desired developmental stage according to morphological characteristics (total length, caudal armature setae) observed via microscopy, and used for experiments.

3.2.2 AQUARIUM EXPERIMENTS (II)

Aquarium experiments were conducted to determine the effects of turbidity on the feeding of zooplanktivorous sticklebacks
and roach. All experiments were carried out in a temperature-controlled indoor chamber in 10 L polypropylene tanks, filled with 10 µm filtered sea water and covered laterally to avoid visual distraction (Fig. 4). Light was provided from above by fluorescent tubes and mean light intensity was measured using a LI-1400 data logger equipped with a LI-192SA quantum sensor (Li-Cor Biosciences; www.licor.com/). Turbidity was achieved in the experimental units by adding sieved natural clayish sediment collected with an Ekman grab sampler from a nearby littoral area. In addition to the clear water control (< 1 NTU), two turbidity treatments were created based on preliminary experiments: medium (45-50 NTU, mean 47.16 ± 0.36 SE) and high (75-80 NTU, mean 77.38 ± 0.35 SE)

Fig 3. Map of the Tvärminne Archipelago on the southwest coast of Finland, northern Baltic Sea showing the location of the Tvärminne Zoological Station and littoral field sites (I). Sites are numbered 1 – 31 from the outer to the inner archipelago respectively. The traditional zonation of the archipelago is depicted with the abbreviations OZ (outer archipelago zone), IZ (inner archipelago zone), MZ (mainland zone) and SZ (sea zone).
Fig 4. Photographs of the setup of the aquarium experiments (II) and the in situ mesocosms (III).
turbidity. Turbidity levels can be as high as 45 NTU in the Baltic Sea archipelago (Granqvist & Mattila 2004). The highest treatment represented a level not currently recorded in the area, although higher turbidities have been recorded in subtropical and temperate estuaries (e.g. Cyrus & Blaber 1987; Maes et al. 1998).

In each experiment, 40 plankters of respective prey types were released into an experimental tank containing one individual fish. The adjusted density of zooplankton corresponds to the composition and density of the natural zooplankton populations in littoral areas of the surrounding archipelago. The predetermined feeding time was 30 minutes, after which fish were dissected. Eight replicates of each zooplanktivore group (male stickleback, female stickleback, juvenile roach) were conducted in the control (clear) and in each turbidity treatment (medium, high) giving a total of 72 experiments. Roach data were not included in paper II.

### 3.2.3 MESOCOSM EXPERIMENTS (III)

Mesocosms were used to investigate the differential effects of zooplanktivorous sticklebacks and roach on a natural zooplankton community. The experiments were carried out in nine UV-resistant 2225 L polyethylene enclosures, placed at a depth of 0.9 – 1.1 m in a shallow bay in the vicinity of the TZS (Fig. 4). The two study periods took place in June (spring) and August (summer) with experimental periods lasting 16 days. The plankton community in each enclosure consisted of a mixture of the natural surrounding seawater community and additional zooplankton acquired from the nearby area, to maximize both density and diversity of the experimental community. The mixture created was calculated to be equivalent to ten times the current natural density of zooplankton. This was to enable the detection of changes in diversity and prevent complete depletion of any particular prey type, since zooplankton were not replaced during the experiments. Equal aliquots of the plankton mixture were added to each enclosure and allowed to settle for five hours before fish were released into the enclosures.

Three fish were released into each of six enclosures, so that three enclosures contained sticklebacks and three contained roach, which was equivalent to approximate fish densities in local natural conditions, determined from previous surveys. An additional three fishless enclosures served as controls, giving a total of three treatments. Zooplankton in the enclosures was sampled using a 2.85 L Limnos water sampler before releasing the fish (day 1), and on days 4, 10 and 16 of the 16-day experiment.

### 3.2.4 NAUPLIUS FEEDING EXPERIMENTS

A series of functional response experiments was carried out on Paracartia grani nauplii using the following algae: the haptophyte
Isochrysis galbana, the dinoflagellates Heterocapsa sp., Gymnodinium litoralis and Akashiwo sanguinea, the diatom Thalassiosira weissflogii, the cryptophyte Rhodomonas salina, and the heterokontophyte Nannochloropsis oculata. Three to seven concentrations of each suspension were prepared, and the range of algal concentrations was obtained by successive dilution of stock cultures. The suspensions were adjusted using a Coulter Multisizer particle counter. Three initial, three control (algae only) and three experimental (algae and nauplii) bottles were filled with prey suspension. Nauplius densities were adjusted according to algae type and concentration, and ranged from \(~12 – 390\) individuals per bottle. The control and experimental bottles were sealed with plastic foil to prevent bubble formation, capped, and mounted on a plankton wheel (0.2 rpm), while initial bottles were sampled immediately to determine initial prey concentrations. Incubation took place for approximately 24 hours, at 18°C with a 12:12 light:dark cycle. After incubation, nauplii were removed from the bottles, preserved using acidic Lugol’s solution, counted and measured. Cell concentrations in the algal suspensions were immediately determined using a Coulter Multisizer particle counter, or alternatively counted under an inverted microscope from preserved samples. N. oculata cell concentrations were estimated using spectrophotometric determination of chl \(a\) and pheo-pigments. Experiments using plurialgal mixtures were also conducted to determine possible interference and selectivity patterns in feeding. These were combinations of 1) I. galbana and G. litoralis and 2) I. galbana and Heterocapsa sp. In the mixed suspensions, five mid-level cell concentrations established from the functional response experiments, of I. galbana were used, and a steady concentration of a secondary alga (Heterocapsa sp. or G. litoralis) was added. Incubations were conducted as above.

3.3 LABORATORY ANALYSES AND MICROSCOPY

Turbidity (in nephelometric turbidity units, NTU) was determined using a standard turbidity meter (Hach 2100P; Hach Co., Loveland, CO, USA) (I, II). Temperature and salinity (VWR EC300 Portable conductivity, salinity and temperature instrument) were measured from separate water samples in mesocosm and field samples (I, III). Salinity is reported using the Practical Salinity Scale. Nutrient concentrations (total nitrogen [TN], total phosphorus [TP]) were determined according to methods by Koroleff (1979) (I, III). To determine algal biomass (expressed as chl \(a\)), 200 ml of sample water was filtered (GF/F filter, 25 mm) and the filters frozen until further analysis. Chlorophyll was extracted from the filters using 5 ml of ethanol, and the solutions read with a spectrophotometer (I, III). Carbon content of algae and nauplii were estimated at TZS using mass spectrometry (Europa Scientific ANCA-MS 20-20 C/N analyzer) from samples which had been filtered onto pre-combusted 25mm GF/C filters, dried
and packed into cryovials with vanadium pentoxide (IV).

Zooplanktivore stomach content analyses were carried out under a binocular microscope (II). Sticklebacks were dissected, their gender determined and the stomach contents were identified and counted under a binocular microscope. The buccal cavity and esophagus were flushed with water to ensure that all consumed zooplankters were accounted for. For cross-referencing with stomach contents, water from the experimental tanks was filtered through a 50 µm net and the remaining zooplankters were counted. Water samples were used to quantify roach consumption data, due to the cyprinid pharyngeal teeth, which macerated prey items and made quantification from the gut content less accurate.

The identification and quantification (ind L⁻¹) of zooplankton from multispecies samples was conducted using an inverted microscope (I, III). Zooplankton samples were divided into appropriate subsamples using a Folsom plankton splitter (either ½, ¼ or ⅛ divisions) due to high zooplankton densities. Individuals were identified to the lowest possible taxonomical level and life stages of copepods were documented as calanoid/cyclopoid nauplii, calanoid/cyclopoid copepodites or adults, where only adults were identified to the species or genus level.

3.4 DATA ANALYSIS

3.4.1 MEASURES OF ZOOPLANKTIVORE PREY SELECTIVITY, ZOOPLANKTON SIZE, BIOMASS AND DIVERSITY

Prey selectivity (II) was determined by calculating Chesson’s α (Chesson 1978) as a selectivity index:

\[
ai = \frac{\ln (\frac{n_{i0} - r_i}{n_{i0}})}{\sum_{i=1}^{m} \ln (\frac{n_{i0} - r_i}{n_{i0}})}, \quad i = 1, \ldots, m
\]

(where \(n_{i0}\) is the number of prey items \(i\) present at the beginning of foraging, \(r_i\) is the number of items of food type \(i\) in the consumer’s diet, \(m\) is the number of food categories available). Values above and below \(1/m\) (in this case 0.33) indicate positive and negative selection respectively.
Mean weighted size (MWS, III) was used as a measure of zooplankton community size changes, and calculated for crustaceans and dominant rotifer species as follows:

\[
\frac{\sum_{i=1}^{n}(L_i \times D_i)}{\sum_{i=1}^{n}(D_i)}
\]

where \(L_i\) is the mean length of species \(i\) in a sample and \(D_i\) is the density of species \(i\) in that sample.

Functional diversity (FD) values were calculated from trait data. Zooplankton traits were chosen to reflect potential effects on ecosystem function, and in this case, traits that describe resource use were selected. Traits included: 1) trophic group based on prey type (herbivore, omni-herbivore, herbi-detritivore, omni-carnivore and carnivore, where preying on heterotrophic protists was considered herbivory since direct ingestion of ciliates was ambiguous for some cladoceran groups) 2) feeding type (suspension, suspension/surface, suspension/ambush, B/D/C/S filtration [DeMott and Kerfoot 1982] and raptorial) and 3) prey size range. Trait information and values were taken from literature, so that only crustaceans and rotifers for which sufficient information exists were used for the analysis. Qualitative measures were entered as rank categories (from herbivore to carnivore and from passive forms of feeding [suspension] to more active ones [raptorial]). Trait values

\[
H' = \sum_{i=1}^{R} P_i \log P_i
\]

where \(P_i\) is the proportion of individuals belonging to the \(i\)th species.

Species/group abundances (I, III) were calculated as individuals L\(^{-1}\) and converted to biomasses (μg L\(^{-1}\) wet weight) (I) according to unpublished calculations from the Finnish Institute of Marine Research based on length measurements.

The Shannon-Weaver diversity index and FD (sensu Petchey and Gaston 2002) were used as measures of taxonomic and functional diversity, respectively (I, III). The Shannon-Weaver index accounts for the abundance and evenness of species present, and is calculated as follows:
were standardized, to represent a starting point situation where the biological variation within each trait was equally important.

A dendrogram depicting the between-group functional relationships was generated using hierarchical clustering analysis (standardized Euclidean distances and average linkage), resulting in groups of functional effect types. In this case, the groups were of zooplankton genera with similar effects on trophic transfer. A functional dendrogram of resource use of common Baltic Sea littoral crustaceans is shown in Fig. 5. \( FD \) values were calculated as the total branch length needed to join all groups in an assemblage, and were standardized to range between 0 (assemblages composed of 1 species) and 1.
Fig 5. A dendrogram produced by hierarchical clustering analysis of typical Baltic Sea coastal zooplankton, showing four functional groups of planktonic crustaceans according to resource use. Data from study I.

Zooplankton group

00.51.01.52.02.53.0

Distance

1

2

3

4

Cercopagis pengoi
Megacyclops spp
Mesocyclops spp
Thermocyclops spp
Cyclops spp
Acartia bifilosa
Acartia longiremis
Acartia tonsa
Temora longicornis
Evadne nordmanni
Evadne anonyx
Pleopsis polyphemoides
Podon leuckarti
Harpacticoida
Eurytemora hirundoides
Eurytemora affinis
Daphnia cucullata
Daphnia cristata
Diaphanosoma brachyurum
Ceriodaphnia quadrangula
Ceriodaphnia pulchella
Eubosmina spp
Chydorus sphaericus
Alona spp

Cyclopoida spp
3.4.2 INGESTION AND CLEARANCE RATES

Nauplius ingestion and clearance rates in feeding experiments were determined according to equations from Frost (1972) (IV). Feeding parameters (maximum filtration rate $F_{\text{max}}$, maximum ingestion rate $I_{\text{max}}$ and half saturation constant $K_m$) were derived from Holling functional response fits. Cell counts were converted into carbon and nitrogen amounts using conversion factors derived from mass spectrometry measurements, and daily ration ($\%$ body carbon/nitrogen ingested d$^{-1}$ nauplius$^{-1}$) was calculated from these.

3.4.3 STATISTICAL METHODS

Univariate methods were employed to test for differences in zooplanktivore prey consumption and selectivity, patterns in zooplankton abundance and size, and differences in diversity measures. The effects of turbidity treatment and species on total prey consumption were assessed using a two-way ANOVA on square root transformed data ($\sqrt{(x +5)}$), with Tukey’s HSD post-hoc analyses (II). The effects of turbidity on total prey consumption of stickleback and roach were tested using one-way ANOVA with Tukey’s HSD post-hoc analysis and Kruskal-Wallis with pairwise comparisons respectively (II). Prey selectivity was examined with the Chi-square goodness-of-fit test ($\chi^2 = \sum (O_i - E_i)^2/E_i$) (II). Differences between the sexes of stickleback in total prey consumption in response to turbidity changes were tested using a two-way ANOVA with Tukey’s HSD post-hoc analyses (II). Differences between sexes in each prey item consumed were tested using a one-way ANOVA; differences in selectivity were tested for each prey type with a two-way ANOVA with Tukey’s HSD post-hoc analyses (II). Repeated measures ANOVA (RMA) was used to compare experimental patterns of zooplankton abundance in mesocosms (III). One-way ANOVA and RMA were used to compare differences in mean weighted zooplankton size and the temporal patterns of size change, respectively (III). RMA and one-way ANOVA were used to compare patterns in zooplankton diversity measures in the field and in mesocosms (I, III). General linear modeling and generalized additive modeling (GAM) were used to model diversity values against environmental variables of the field sites (I). Nonlinear least-squares regression was used to fit functional response curves for nauplius feeding experiments (IV).

Multivariate methods were used to examine zooplankton community structure in the field and in mesocosms, and to visualize relationships between environment and biota. The Bray-Curtis similarity coefficient was applied to create species similarity matrices from zooplankton abundance data. Non-metric multidimensional scaling (nMDS) (I, III) and principal coordinate ordination (PCO) were used to visualize differences in overall zooplankton community structure (III). Analysis of similarities (ANOSIM) was used to test whether the a priori defined archipelago zones formed distinct zooplankton communities that differed from each other (I). Hierarchical
clustering and the SIMPROF procedure were used to identify deviating field sites in terms of community composition (I). The Similarity Percentages (SIMPER) procedure analyzed the contribution of taxa to the mean dissimilarity between samples (I, III). Principal component analyses (PCA) were carried out to portray environmental parameters of field sites (I). To assess the relationship between the plankton assemblage and the environmental parameters PRIMER v6 routines were used. The RELATE routine using the Spearman rank correlation coefficient was used to quantify the relationship, and the BEST procedure was applied to determine which environmental factors best correlate with the species matrix (I). Distance-based linear modeling (DistLM) was used to describe the biota using environmental variables (I). A partly nested permutational MANOVA (PERMANOVA) was run to test for differences in overall community structure between mesocosms (III). SPSS v 21 (2012 IBM), R v 2.10.1 (R Development Core Team 2013) and PRIMER v 6 (PRIMER-E Ltd., Plymouth, UK) were used to analyze the data.
4 MAIN RESULTS

4.1 ENVIRONMENTAL DESCRIPTION OF FIELD SITE

When all environmental data from field sampling sites (1 – 31) were combined from both years (2009 and 2010), a cluster analysis identified five general littoral habitat groups (Table 1). Sites 13 and 16 were not found to fit into any of the environmentally determined groups of habitats. Site 13 was a shallow, extremely sheltered lagoon, which grouped most closely with the similar sites in the MZ, with the exception of its high salinity. Site 16 was a long, relatively exposed beach with high salinity and high algal biomass. However, in terms of zooplankton composition (section 4.2) neither site differed significantly from other sites in the zone (site 13) or in the immediate geographic proximity (site 16) regardless of sampling time. This was presumably related to the fact that communities were to a great extent determined by salinity. Environmental data for all sites and combined for 2009 and 2010 are summarized in Fig. 6 and depicted in detail in paper I.

Table 1. Field site environmental data combined from years 2009 and 2010. Habitat groups (I-V, shown with the associated sites) were determined by cluster analysis of environmental characteristics of sites in the Tvärminne Archipelago.
Fig 6. Environmental variables from all field sites, with mean values ± SE from 2009 and 2010 where possible. Macrophyte coverage (2009), algal biomass (2010), and nutrient data (2010) are from a single year. Wave exposure indices do not differ yearly. Data from study I.
4.2 Littoral community composition and diversity (I)

Altogether 64 zooplankton taxa (including species, genera and crustacean life stages, recorded as nauplii/copepodites for copepods and juveniles for cladocerans) were identified in both time periods, although the groups were not concurrent between years. Total abundance was higher in the earlier 2009 sampling period compared to the later sampling period in 2010. High abundance was associated with high densities of calanoid nauplii or rotifers in both years, and additionally in the 2010 sampling the dominant calanoid copepods. Highest biomasses were associated with calanoid nauplii, dominant rotifers (*Synchaeta, Keratella*) or dominant crustaceans (cladocerans *Pleopsis polyphemoides* and *Eubosmina*, copepods *Acartia, Eurytemora*, and calanoid/cyclopoid copepodites). Combined abundance and biomass values from both sampling periods for all field sites are shown in Fig. 7.

The nMDS ordinations consistently grouped OZ and IZ sites together according to their zooplankton composition, with a transitional zone at sites 24 – 25, and the low salinity MZ sites clearly separated from the archipelago zones. The ANOSIM did not show differences between IZ and OZ in 2009 ($R = 0.069, p = 0.25$), but distinguished MZ from the two archipelago zones (IZ and MZ $R = 0.644, p = 0.006$ and OZ and MZ $R = 0.835, p = 0.001$), and conversely all the zones from each other in 2010 ($R = 0.623, p = 0.001$). Typical species per zone differed between sampling periods and are summarized in Table 2. Cluster analyses without a priori grouping for the zooplankton community distinguished only two primary clusters: the brackish area (with salinity > 4) and the freshwater area (with salinity < 4) (Fig. 8). The SIMPROF procedure consistently identified two sites (20 and 31) which differed in composition from other sites in their respective zones. There was generally low correlation between the abiotic and biotic resemblance matrices. Main results from the multivariate routines are summarized in Table 3. The species matrices of the different sampling periods were similar, indicating approximate temporal consistency in spatial patterns ($\rho = 0.52, p = 0.001$).
Fig. 7. Mean density (a) and biomass (b) of zooplankton in field sites from combined 2009 and 2010 sampling. Sites 16 and 30 are based on data from 2009 and 2010 only, respectively. ‘Copepods’ include adults and copepodites; ‘others’ include copepod nauplii and meroplanktonic larvae. Data from study I.
Table 2. Main groups of zooplankton typifying the salinity zones of a coastal Baltic Sea area according to SIMPER analysis during two sampling years (OZ = outer archipelago zone, IZ = inner archipelago zone, MZ = mainland zone)

<table>
<thead>
<tr>
<th>Zone</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
</table>

Table 3. Showing results from multivariate routines performed on a zooplankton species matrix and associated environmental variables of the 2009 – 2010 field sites. Results from the RELATE (correlation between the zooplankton species matrix and the environmental variables) and BEST (environmental factors which best correlate with the species matrix) routines are shown, as well as the variables included in and the associated $R^2$ value for the best model determined by distance-based linear modeling.

<table>
<thead>
<tr>
<th>Year</th>
<th>RELATE correlation</th>
<th>BEST variables</th>
<th>BEST correlation</th>
<th>DistLM variables</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>0.361</td>
<td>Salinity, turbidity</td>
<td>0.707/0.661</td>
<td>Salinity, turbidity, temperature</td>
<td>0.395</td>
</tr>
<tr>
<td>2010</td>
<td>0.258</td>
<td>Salinity/ Salinity, chl a</td>
<td>0.686/0.582</td>
<td>Salinity</td>
<td>0.267</td>
</tr>
</tbody>
</table>
Fig. 8. Results of a hierarchical cluster analysis of Tvärminne Archipelago coastal field sites 1 – 31 based on zooplankton communities in (a) 2009 and (b) 2010, showing the two main clusters of the brackish area (IZ/OZ) and the freshwater area (MZ). Data from study I.
The functional dendrogram resulted in four functional groups of planktonic crustaceans (Fig. 5). Using the a priori defined zones, crustacean FD was significantly higher in the MZ compared to the other two zones (one way ANOVA $F_{2,58} = 13.478, p < 0.001$). General linear models were fitted to the data with FD as the response variable and salinity, temperature, turbidity, and exposure as predictors. For the 2009 data the model included only salinity as significant, with an inverse relationship between FD and salinity ($R^2 = 0.56$, 28 df, $p < 0.001$). In 2010 FD decreased non-linearly with salinity and a smoothing function was applied. Salinity ($p = 0.002$), temperature ($p = 0.002$) and turbidity ($p = 0.001$) were all significant in the model ($R^2 = 0.73$).

All zooplankton groups were considered in measuring taxonomic diversity ($H'$). A GAM (Generalized Additive Model) was fitted to the data, with $H'$ as response variable and salinity, turbidity and exposure as well as total zooplankton biomass as predictors. Only salinity was significant. Incorporating nonlinear effects improved the model significantly, and it explained 26.9% of the deviance ($p = 0.004$). $H'$ increased with salinity until 5, at which point it decreased. The pattern in total biomass was similar, and there was a weak correlation between taxonomic diversity and biomass (Pearson’s correlation $r(58) = 0.317, p = 0.01$).

### 4.3 PREDATION BY ZOOPLANKTIVOROUS FISH

#### 4.3.1 EFFECTS OF TURBIDITY ON CONSUMPTION AND SELECTION OF ZOOPLANKTON PREY (II)

Total prey consumption in response to increasing turbidity was found to differ between sticklebacks and roach (two-way ANOVA, species*turbidity treatment, $F_{2,72} = 52.5, p < 0.001$) (Fig. 9). Consumption by sticklebacks declined with increasing turbidity (one-way ANOVA, $F_{2,21} = 44.430, p < 0.001$), rendering it lower in the high turbidity treatment than in the control and the medium treatment ($p < 0.001$ in both). Conversely, consumption by roach increased in high turbidity (Kruskal-Wallis, $H = 15.521, p < 0.001$).
In sticklebacks, consumption of both the daphnid (one-way ANOVA $F_{2,45} = 10.298, p = < 0.01$) and the copepods (one-way ANOVA, $F_{2,45} = 8.827, p < 0.05$) were significantly lower in high turbidity. Sticklebacks showed a high selectivity for the daphnid in all treatments, which increased in elevated turbidity (Fig. 10). Selectivity for the smaller copepod species proved negative in the control and the negative selection intensified with increasing turbidity (Fig. 10). When the two copepod groups were considered, sticklebacks selected *Acartia* or alternatively rejected *Eurytemora* in the clear water control (chi-square test, $\chi^2 = 17.36, p < 0.001$). Roach showed positive selection for the daphnid in the clear water control (chi-square test, $\chi^2 = 10.11, p < 0.01$), but in the turbidity treatments no significant selection for any prey species was found ($p > 0.05$) (Fig. 10). When only copepods were considered, roach appeared to display no significant selection for either group (all $p > 0.5$).
Fig. 10. Mean Chesson’s α index (Chesson, 1978) for consumption of Daphnia longispina (white), Acartia sp. (striped) and Eurytemora sp. (black bars) for (a) stickleback and (b) roach in different turbidity treatments. The dashed line shows the value of 1/n, where values above the line indicate positive selection and values below the line indicate negative selection. Data for (a) from paper II.
4.3.2 ZOOPLANKTIVOROUS PREDATION AND EFFECTS ON PREY COMMUNITY: ZOOPLANKTON SIZE, SPECIES COMPOSITION AND DIVERSITY (III)

In the mesocosm experiments, community effects of predation were found to be dependent on predator type as well as initial community structure (i.e. seasonal variation). Overall, community size structure was clearly shifted towards larger species in the absence of predation. An nMDS of the combined community data showed the successional differences in zooplankton community between control and predator treatments, and notably the development of the spring control community towards a large-bodied summer community (Fig. 11).

**Fig. 11.** NMDS ordination of zooplankton communities (square root transformed data) combined for spring and summer mesocosm experiments. Numbers represent sampling days 1, 4, 10 and 16. Letters represent control (C), stickleback (S) and roach (R) treatments. Superimposed clusters are based on Bray-Curtis similarities at levels of 60% (solid line) and 80% (dashed line). Arrows indicate direction of increasing abundances of zooplankton groups which contributed most to differences between communities. Data modified from paper III.
In the spring, initial total abundance of individuals was high due to representation by numerous small-sized taxa (Fig. 12). High total abundance was reflected in high densities of small-bodied zooplankton groups, such as microzooplankton and rotifers, while low total abundance was associated with high densities of larger crustaceans (Fig. 12). Microzooplankton and rotifer abundances were determined by time and treatment (Table 4), and stickleback enclosures had a significantly higher abundance of these groups than the control ($p < 0.01$ and $p < 0.005$ respectively). Patterns in cladoceran and copepod abundance varied between treatments, as shown by the significant time*treatment interactions (Table 4). Crustacean abundance in predator enclosures was significantly lower than in the control towards the end of the experiment (one-way ANOVA, day 10 $F_{2,8} = 23.033$, $p < 0.005$, and day 16 $F_{2,8} = 9.124$, $p < 0.05$ for cladocerans; day 10 $F_{2,8} = 19.423$, $p < 0.005$, and day 16 $F_{2,8} = 136.416$, $p < 0.001$ for copepods).

**Fig. 12.** Total zooplankton abundance in mesocosm experiments with zooplanktivore treatments (including microzooplankton). Abundances are plotted over the four sampling dates to show the time*treatment interaction from the repeated-measures ANOVA. Note distinct axis scales. Data from paper III.
Table 4. Summary of the results of a two-factor ANOVA with repeated measures (RMA) for the analysis of differences in weighted size, total abundance, group abundances, and two measures of diversity (the Shannon–Weaver diversity index, $H'$, and functional diversity, $FD$) across time and predator treatment in the spring and summer periods of a mesocosm experiment.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
<th>df</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Weighted size</td>
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</tr>
<tr>
<td>Time</td>
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<td>67.761</td>
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<td>3</td>
<td>11.313</td>
<td>&lt;0.001</td>
</tr>
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<td>0.211</td>
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<td>Time*treatment</td>
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<td>5.702</td>
<td>0.002</td>
</tr>
<tr>
<td>Total abundance</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>5.654</td>
<td>0.007</td>
<td>3</td>
<td>27.771</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>0.001</td>
<td>2</td>
<td>5.141</td>
<td>0.05</td>
</tr>
<tr>
<td>Time*treatment</td>
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<td>0.905</td>
<td>0.513</td>
<td>6</td>
<td>3.376</td>
<td>0.021</td>
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<tr>
<td>Microzoopl. abundance</td>
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</tr>
<tr>
<td>Time</td>
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<td>0.01</td>
<td>3</td>
<td>3.257</td>
<td>0.121</td>
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<tr>
<td>Treatment</td>
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<td>0.008</td>
<td>2</td>
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<td>0.740</td>
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<tr>
<td>Time*treatment</td>
<td>6</td>
<td>4.592</td>
<td>0.051</td>
<td>6</td>
<td>0.372</td>
<td>0.706</td>
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<tr>
<td>Rotifer abundance</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>20.282</td>
<td>&lt;0.001</td>
<td>3</td>
<td>40.424</td>
<td>&lt;0.001</td>
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<td>Time*treatment</td>
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<td>0.401</td>
<td>6</td>
<td>7.495</td>
<td>0.015</td>
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<td>Cladoceran abundance</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>1.7</td>
<td>1.864</td>
<td>0.206</td>
<td>3</td>
<td>2.214</td>
<td>0.122</td>
</tr>
<tr>
<td>Treatment</td>
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<td>0.006</td>
<td>2</td>
<td>4.576</td>
<td>0.062</td>
</tr>
<tr>
<td>Time*treatment</td>
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<td>6.078</td>
<td>0.01</td>
<td>6</td>
<td>2.676</td>
<td>0.049</td>
</tr>
<tr>
<td>Copepod abundance</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>23.236</td>
<td>&lt;0.001</td>
<td>1.4</td>
<td>8.556</td>
<td>0.014</td>
</tr>
<tr>
<td>Treatment</td>
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<td>29.157</td>
<td>0.001</td>
<td>2</td>
<td>2.383</td>
<td>0.173</td>
</tr>
<tr>
<td>Time*treatment</td>
<td>6</td>
<td>18.383</td>
<td>&lt;0.001</td>
<td>2.8</td>
<td>4.409</td>
<td>0.041</td>
</tr>
<tr>
<td>Taxonomic diversity ($H'$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>6.363</td>
<td>0.004</td>
<td>3</td>
<td>28.988</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>48.561</td>
<td>&lt;0.001</td>
<td>2</td>
<td>0.303</td>
<td>0.750</td>
</tr>
<tr>
<td>Time*treatment</td>
<td>6</td>
<td>5.188</td>
<td>0.003</td>
<td>6</td>
<td>1.510</td>
<td>0.231</td>
</tr>
<tr>
<td>Functional diversity ($FD$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>1.580</td>
<td>0.229</td>
<td>3</td>
<td>0.458</td>
<td>0.715</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
<td>1.350</td>
<td>0.328</td>
<td>2</td>
<td>0.029</td>
<td>0.972</td>
</tr>
<tr>
<td>Time*treatment</td>
<td>6</td>
<td>3.197</td>
<td>0.026</td>
<td>6</td>
<td>0.966</td>
<td>0.475</td>
</tr>
</tbody>
</table>

Throughout the duration of the spring experiment there were clear differences in zooplankton successional dynamics between treatments, as indicated by the significant time*treatment interaction of the partly-nested PERMANOVA ($F = 6.60$, $p = 0.001$). Segregation of stickleback enclosures from the control as early as the fourth experimental day was apparent (pairwise comparisons $t = 2.52$, $p(MC) < 0.05$). By day 10 predator enclosures clearly differed from the control (pairwise comparisons stickleback $t = 5.36$, $p(MC) = 0.001$ and roach $t = 4.29$, $p(MC) < 0.005$). The main results of the SIMPER analyses show the zooplankton groups which contributed most to the dissimilarities between enclosures, notably the *Eurytemora* and *Acartia* abundances differentiating the predator enclosures (Table 5). A difference between the predator enclosures was detectable, as roach and stickleback enclosures were
segregated into their own distinct groups (pairwise comparisons $t = 1.93$, $p(MC) < 0.05$). On the last sampling day (day 16) of the spring experiment, both predator enclosures were characterized by rotifers and ciliates. Roach enclosures were more diverse, and additionally characterized by calanoid copepod life stages. Both predator enclosures remained significantly segregated from the control (pairwise comparisons stickleback $t = 6.03$, $p = 0.001$, roach $t = 3.63$, $p(MC) < 0.005$), in which typical groups were the dominant calanoid copepods and nauplii.

Table 5. Dissimilarities between treatments on days 10 and 16 of the experiments (spring and summer) displaying species/genera which cumulatively contribute to over 50% of the dissimilarity determined from the SIMPER analysis. Species/genera are grouped as microzooplankton (micro), rotifers (rot), cladocerans (clad) and copepods (cop). Direction of difference describes whether the group abundance is higher (+) or lower (-) in the second treatment of the treatment pair compared to the first.

<table>
<thead>
<tr>
<th>Period/Day</th>
<th>Treatment pair</th>
<th>Dissimilarity percentage</th>
<th>Species/group</th>
<th>Percentage contribution</th>
<th>Direction of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring 10</td>
<td>Control – Stickleback</td>
<td>58.56%</td>
<td>Tintinnopsis lobiancoi (micro)</td>
<td>41.57%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Synchaeta spp. (rot)</td>
<td></td>
<td></td>
<td>10.14%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pleopsis polyphemoides (clad)</td>
<td>33.04%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Keratella cruficormis (rot)</td>
<td></td>
<td></td>
<td>12.36%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.02%</td>
<td>-</td>
</tr>
<tr>
<td>Spring 10</td>
<td>Control – Roach</td>
<td>47.58%</td>
<td>Tintinnopsis lobiancoi (micro)</td>
<td>37.75%</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Synchaeta spp. (rot)</td>
<td></td>
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<td>5.25%</td>
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<tr>
<td></td>
<td>Eurytemora spp. (cop)</td>
<td></td>
<td></td>
<td>4.84%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Vorticella spp. (micro)</td>
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<td>4.70%</td>
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</tr>
<tr>
<td>Spring 10</td>
<td>Stickleback – Roach</td>
<td>22.30%</td>
<td>Tintinnopsis lobiancoi (micro)</td>
<td>34.98%</td>
<td>+</td>
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<tr>
<td></td>
<td>Synchaeta spp. (rot)</td>
<td></td>
<td></td>
<td>10.63%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Keratella cruciformis (rot)</td>
<td></td>
<td></td>
<td>9.24%</td>
<td>+</td>
</tr>
<tr>
<td>Spring 16</td>
<td>Control – Stickleback</td>
<td>71.57%</td>
<td>Tintinnopsis lobiancoi (micro)</td>
<td>34.52%</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Synchaeta spp. (rot)</td>
<td></td>
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<td>15.92%</td>
<td>+</td>
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<td>Keratella cruciformis (rot)</td>
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<td>10.82%</td>
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<td>Control – Roach</td>
<td>54.54%</td>
<td>Tintinnopsis lobiancoi (micro)</td>
<td>34.98%</td>
<td>+</td>
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<td></td>
<td>Synchaeta spp. (rot)</td>
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<td>10.63%</td>
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<td></td>
<td>Keratella cruciformis (rot)</td>
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<tr>
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<td>calanoid nauplius (micro)</td>
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<td>6.65%</td>
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<td>Period/Day</td>
<td>Treatment pair</td>
<td>Dissimilarity percentage</td>
<td>Species/group Percentage contribution</td>
<td>Direction of difference</td>
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</tr>
<tr>
<td>------------</td>
<td>-----------------</td>
<td>--------------------------</td>
<td>---------------------------------------</td>
<td>------------------------</td>
<td></td>
</tr>
<tr>
<td>Summer 10</td>
<td>Control – Stickleback</td>
<td>34.52%</td>
<td>Calanoid nauplius (micro) 16.55% +</td>
<td></td>
<td></td>
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<td></td>
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<td>Synchaeta spp. (rot) 15.92% +</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Calanoid copepodite (cop) 9.37% +</td>
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<td>Eubosmina spp. (clad) 8.79% -</td>
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<tr>
<td>Summer 10</td>
<td>Control – Roach</td>
<td>34.48%</td>
<td>Synchaeta spp. (rot) 15.30% +</td>
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<td></td>
<td></td>
<td></td>
<td>Keratella quadrata (rot) 15.10% +</td>
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<td></td>
<td></td>
<td></td>
<td>Calanoid nauplius (micro) 10.82% +</td>
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<td></td>
<td></td>
<td></td>
<td>Acartia spp. (cop) 9.02% -</td>
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<tr>
<td>Summer 16</td>
<td>Stickback – Roach</td>
<td>22.21%</td>
<td>Calanoid nauplius (micro) 11.94% -</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Keratella quadrata (rot) 10.70% +</td>
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<td></td>
<td>Calanoid copepodite (cop) 10.22% -</td>
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<td></td>
<td>Synchaeta spp. (rot) 9.73% +</td>
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<td></td>
<td>Eubosmina spp. (clad) 6.61% -</td>
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<td></td>
<td></td>
<td></td>
<td>Pleopsis polyphemoides (clad) 5.46% +</td>
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<tr>
<td>Summer 16</td>
<td>Control – Stickleback</td>
<td>41.27%</td>
<td>Keratella quadrata (rot) 16.05% +</td>
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<td></td>
<td>Calanoid nauplius (micro) 11.70% +</td>
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<td></td>
<td></td>
<td></td>
<td>Eubosmina spp. (clad) 11.01% -</td>
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<td></td>
<td></td>
<td></td>
<td>Keratella cochlearis (rot) 8.48% +</td>
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<td></td>
<td></td>
<td></td>
<td>Calanoid copepodite (cop) 7.46% +</td>
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<tr>
<td>Summer 16</td>
<td>Control – Roach</td>
<td>47.12%</td>
<td>Keratella quadrata (rot) 17.03% +</td>
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<td></td>
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<td></td>
<td>Calanoid nauplius (micro) 11.58% +</td>
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<td></td>
<td></td>
<td>Keratella cochlearis (rot) 11.49% +</td>
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<td></td>
<td></td>
<td></td>
<td>Eubosmina spp. (clad) 11.43% -</td>
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<tr>
<td>Summer 16</td>
<td>Stickback – Roach</td>
<td>23.85%</td>
<td>Acartia spp. (cop) 14.26% -</td>
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<td></td>
<td></td>
<td></td>
<td>Keratella quadrata (rot) 12.01% +</td>
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<td></td>
<td></td>
<td></td>
<td>Keratella cochlearis (rot) 8.98% +</td>
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<td></td>
<td></td>
<td></td>
<td>Eubosmina spp. (clad) 7.81% -</td>
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<td></td>
<td></td>
<td></td>
<td>Synchaeta spp. (rot) 6.46% +</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Euchlanis dilatata (rot) 5.46% +</td>
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</table>
Initial group abundances in the summer reflected the large-bodied community, with lower densities of microzooplankton and rotifers and higher densities of crustaceans compared to the spring period. Total zooplankton abundance increased in all enclosures with time, as opposed to the decreasing trend in the spring, but the response pattern differed with treatment, as indicated by the significant time*treatment interaction (Fig. 12, Table 4). Correspondingly to the spring experiment, the significant time*treatment interaction revealed that the succession of cladocerans and adult copepods differed between treatments (Table 4). Adult copepods were slightly more abundant in stickleback enclosures throughout the experiment, except on day 10, when abundance was significantly higher in the control (one-way ANOVA $F_{2,8} = 13.862, p < 0.01$).

The significant time*treatment interaction indicated differences in zooplankton succession between treatments (partly-nested PERMANOVA, $F = 2.30, p = 0.001$). Communities in predator enclosures differed from the control from day 10 onwards (pairwise comparisons stickleback $t = 2.32, p(MC) < 0.05$ and roach $t = 2.74, p(MC) < 0.01$). On day 16 roach enclosures were very homogenous and least similar to the control (pairwise comparisons, $t = 3.32, p(MC) < 0.05$), which also significantly differed from stickleback enclosures (pairwise comparisons, $t = 2.25, p(MC) < 0.05$) (Table 5). The cladoceran Podon leuckartii was unique to the control. Diversity values differed throughout the spring experiment depending on treatment (Table 4). Taxonomic diversity decreased in stickleback enclosures, and on the last sampling days was significantly lower than in the other treatments (one-way ANOVA, day 10 $F_{2,6} = 231.893, p < 0.001$ and day 16 $F_{2,6} = 6.455, p < 0.05$). Functional diversity was also significantly lower in the stickleback than control enclosures on day 16, in direct opposition of the initial sampling (one-way ANOVA, $F_{2,6} = 7.011, p < 0.05$). Predation had no effect on either diversity measure in the summer experiment.

4.4 ZOOPLANKTON GRAZING: FEEDING AND SELECTIVITY OF COPEPOD NAUPLII (IV)

All data from unialgal experiments were fitted to Holling type II or type III equations. depending on the pattern of clearance rates at low prey concentrations (Fig. 13). The functions used were as follows:

Holling type II: $I = (C \cdot I_{\text{max}}) / (C + K_m)$ and $F = a / (C + b)$

Holling type III: $I = (I_{\text{max}} \cdot C^2) / (C^2 + K_m^2)$ and $F = I_{\text{max}} \cdot C / (C^2 + K_t^2)$

where $I$ is the ingestion rate and $I_{\text{max}}$ the maximum ingestion rate (cells ind$^{-1}$ d$^{-1}$), $F$ is the clearance rate (ml ind$^{-1}$ d$^{-1}$), $C$ is the concentration of prey (cells ml$^{-1}$), $a$ and $b$ are prey specific constants, $K_m$ is the half saturation constant, and $K_t$ is the food concentration at which maximum clearance rate is reached. Maximum
clearance rates \( F_{\text{max}} \) were highest for \( T. \text{weissflogii} \) and lowest for \( I. \text{galbana} \), indicating that the prey size spectrum peaked at an approximate prey:predator size ratio of 0.08. The daily rations (in % body carbon and nitrogen ingested day\(^{-1}\) nauplius\(^{-1}\)) were highest for ingestion of the dinoflagellate \( Heterocapsa \) sp. (up to 335% and 276% for C and N respectively) and lowest for \( R. \text{salina} \) (92% and 65% for C and N respectively). In the plurialgal mixtures using \( I. \text{galbana} \) as a baseline prey, maximum clearance rate for \( I. \text{galbana} \) was up to 32% lower than in unialgal suspensions, and clearance rate of the secondary alga depended on prey type, rendering lower (\( Heterocapsa \) sp.) or higher (\( G. \text{litoralis} \)) values than estimated from the Holling fits.
Ingestion rate (cells/ind/day)

Prey concentration (cells/ml)

**I. galbana**

Type III response

\[ I = \frac{953 \times C^2}{C^2 + 22830^2} \]

R sq = 0.99

**R. salina**

Type III response

\[ I = \frac{117 \times C^2}{C^2 + 142^2} \]

R sq = 0.67

**Heterocapsa sp.**

Type II response

\[ I = \frac{1232 \times C^2}{C^2 + 1840^2} \]

R sq = 0.99

**Type II response**

\[ I = \frac{402 \times C}{C + 572} \]

R sq = 0.78

\[ I = \frac{1043 \times C}{C + 2561} \]

R sq = 0.81

\[ I = \frac{1232 \times C^2}{C^2 + 1840^2} \]

R sq = 0.99
Fig. 13. Showing functional responses (ingestion rate and clearance rate as functions of prey density) of the Paracartia grani nauplius to various microalgal prey: P. grani vs. Isochrysis galbana, Thalassiosira weissflogii, Rhodomonas salina, Heterocapsa sp. and Gymnodinium litoralis. Maximum ingestion rate values (Imax) estimated from the Holling fits are indicated with a dashed circle. Data from paper IV.
5 DISCUSSION

5.1 ZOOPLANKTON IN THE LITTORAL BALTIC SEA

5.1.1 ASPECTS OF DISTRIBUTION

Zooplankton species were not evenly distributed across the salinity gradient (I), as is the general case with estuarine organisms (Segerstråle 1959; Remane & Schlieper 1971). A salinity of 4 was found to be an unambiguous boundary value, which segregated freshwater communities from more marine ones. A corresponding range, from freshwater values up to a salinity of 4, has also been found to define a low salinity estuarine zone in terms of fish and invertebrates (Bulger et al. 1993). Predictably, salinity was the most significant abiotic structuring force on zooplankton composition. Correlations between the abiotic variables and the biota involved either salinity alone (2010) or salinity and turbidity/chl a (2009). Salinity limits and preferences of zooplankton are known to regulate their long-term distribution patterns in the pelagic, and expectedly this appeared to be the case in the littoral as well (Ojaveer et al. 1998; Vuorinen et al. 1998). Factors related to productivity (temperature, trophic state and phytoplankton biomass) have also previously been found to determine zooplankton composition in the Baltic Sea (Johansson 1992; Scheinin & Mattila 2010).

The temporal differences in species composition were considerable, especially concerning the microzooplankton component. The same phenomenon has been found in other studies in estuaries and lagoons associated with the Baltic Sea, whereas succession on a spatial scale has generally been found to be comparatively uniform (Gasiūnaitė & Razinkovas 2004; Scheinin & Mattila 2010 but see Koski et al. 1999a). In this study, the extent and patterns of spatial heterogeneity in species composition on a larger scale remained relatively constant regardless of sampling period, so that the interannual between-site relationships remained similar, even though the respective assemblages differed. Therefore, successional dynamics were clearly portrayed throughout the gradient. Rotifers were particularly pervasive throughout the sampling area, with dominant Keratella species abundant in the MZ in 2009 and in the OZ in 2010. This reflected the general patterns in rotifer spatial succession, which developed from the warmer, sheltered sites in the early sampling to the outer archipelago in the later sampling.

In terms of zooplankton composition, the transition region was at sites 24 and 25, which belonged to either the MZ or the IZ depending on sampling year. Both sites were located at the entrance to the geographical bottleneck between the IZ and the MZ, and had much lower salinity values than the offshore high salinity sites (19 – 23) in the IZ. In general, the zones were differentiated by distinct zone-related taxa (e.g. bivalve larvae in the IZ/OZ, cyclopoids in the MZ), or alternatively by varying densities of the most abundant taxa (e.g. the copepod...
Acartia, cladoceran Eubosmina and Keratella rotifers). Cyclopoids and onychopods are generally limited by salinity (e.g. Jennings et al. 1994; Onbé & Ikeda 1995), but the salinity differences on this gradient were too subtle to directly restrict the distribution of the planktonic crustaceans through strict tolerance limits. This was depicted by the sporadic occurrence of cyclopoids in the OZ and podonid cladocerans in the MZ in salinities > and < 4, respectively. The low between-site variation south of the ecotone supports traditional niche-based theory, by which deterministic factors, including environmental conditions, control local community composition. Deterministic processes are expected to be of higher influence than stochastic processes (e.g. random extinctions or colonizations) in just such harsh fluctuating environmental conditions (Chase 2007; Lepori & Malmqvist 2009).

However, temporally consistent differences were found between sites 20 and 31 and other sites in their respective zones. Site 31 differed from the other sites of the MZ due to its extremely high densities of all life stages and species of cyclopoids and the omnivorous cladoceran Pleopsis polyphemoides, which was absent from other MZ sites. Moreover, a high density and diversity of rotifers, and a distinct lack of calanoid copepods differentiated it from surrounding sites. Compared to other sites in its geographical vicinity, the site had extremely high chl a, and accordingly, eutrophication has been found to strengthen the role of rotifers in estuarine communities (Telesh 2004).

However, this trend was not evident in the other highly eutrophic sites. Chemical pollution, such as pesticides and oil, were other possible segregating factors. Estuarine zooplankton abundance and community structure have been found to be altered by pollution, mainly exhibited as a decrease in copepod density, and specifically in the Gulf of Finland with a reduction in the dominant calanoids Eurytemora and Acartia. (Ojaveer et al. 1998; Uriarte & Villate 2004). This corresponds to the significantly lower calanoid nauplius abundances (2009 and 2010) and lower Eurytemora abundance (2009) at site 31 compared to other MZ sites, and the complete absence of Acartia (2010). However, it is also worth considering that a general decline in mesozooplankton abundance, including abundances of Acartia and Eurytemora, has been observed in the Gulf of Finland in long-term data, which has been attributed to increasing temperature (Suikkanen et al. 2013).

Site 20 was distinct from the other OZ/IZ sites due to high densities of harpacticoids and small cladocerans, and a diverse rotifer population that consisted of species not found in other OZ/IZ sites. Site 20 is classified as a semi-enclosed flad, a brackish lagoon in a geomorphometric evolutionary stage in which it is still in continuous contact with the sea, but with the natural land-uplift process it is in the process of gradually becoming isolated from the sea, with slower sea water influx compared to more open bays (Munsterhjelm 2005). Macrophytes, macroinvertebrate fauna, and fish assemblages have been
found to differ between morphometric developmental stages of bays in the northern Baltic, and zooplankton communities in such shallow bays have been found to be particularly diverse and abundant compared to pelagic areas (Appelgren & Mattila 2005; Hansen et al. 2007; Snickars et al. 2009; Scheinin & Mattila 2010). The discrepancy between this site and the other bays suggests that isolation-related water exchange is also a significant factor in molding coastal zooplankton composition. Preliminary data on fish biomasses, species composition and stomach contents indicate that three-spined sticklebacks occur at the site and readily consume zooplankton (Borg et al. unpublished). The linkages between zooplankton and environmental variables may be less evident in such stable semi-enclosed, isolated areas, where predation by zooplanktivorous fish can result in the efficient top-down control of large crustaceans. Biotic interactions, such as predation and competition, are expected to be more important in shaping community structure in the absence of environmental stress, and accordingly, species adaptations that promote environmental tolerance often trade off with adaptations that promote fitness under conditions of intense biotic interactions (Wellborn et al. 1996). A flad resembles a relatively small, ‘closed’ system, where biotic relationships play a significant role in structuring assemblages because of high interaction potential. This is in line with the low copepod abundance and the high diversity of rotifers, as well as a high abundance of the small grazing cladoceran Ceriodaphnia found at site 20. Predation may indirectly facilitate invasion by species at lower trophic levels, which are otherwise excluded by interactions with the target prey (Holt et al. 1994; Leibold 1996). Ceriodaphnia was uncommon at other sites but may gain a foothold in areas where larger and more actively grazing crustaceans are removed by predation. Similarly, we found fish predation to increase rotifer abundance and prevent intense domination by any particular species in a small-bodied prey community (III). Prey-predator relationships could be a factor in distinguishing this flad site from the others.

5.1.2 ASPECTS OF DIVERSITY

Functional diversity was inversely related to salinity in the field. This is to be expected, because competition structures communities more intensely in these physically less harsh habitats. High functional diversity results from competitive exclusion characterizing interactions among species: Organisms need to feed at different trophic levels, using different temporal patterns and feeding strategies to be able to coexist (Armstrong & McGehee 1976). However, site 20 was repeatedly anomalous regarding the salinity-FD relationship, portraying lower diversity than predicted by salinity alone. This is again concurrent with intense fish predation, which potentially decreases prey diversity (Paine 1966). Additionally, in the later sampling period, turbidity and temperature complicated the salinity-FD relationship,
with low salinity sites exhibiting lower $FD$ values than predicted. These sites had high temperatures towards the end of the summer, which presumably would begin to either directly limit the occurrence of thermophobic crustacean taxa or indirectly decrease longevity (e.g. Altshuler 2011), and hence decrease within-site diversity. This suggests that at a certain temperature threshold, the $FD$-salinity relationship does not hold. Additionally, $FD$ was higher than predicted by salinity alone at sites with high algal biomass, suggesting that increased resources result in higher $FD$ regardless of salinity. In equally shallow lake systems, productivity was generally negatively related to zooplankton functional diversity, but the type of phytoplankton resource was found to be indicative of the response (Barnett & Beisner 2007).

The lowest taxonomic diversity was found in the transition zone from freshwater to brackish water, at sites 24, 25 and 26 in 2009. These sites had high densities of particular rotifer taxa. The dominance of eurytopic species is a common feature in Baltic estuaries (Telesh 2004), and accordingly, all sites with low diversity were dominated by high densities of either *Keratella cochlearis* or *K. quadrata*, regardless of zone or sampling period. In agreement with previous studies in brackish waters and estuaries (Gasiūnaitė 2000; Telesh 2004), our study did not find a linear relationship between salinity and taxonomic diversity of zooplankton. Instead we found similar evidence of high diversity at an intermediate salinity, in this case 5, after which diversity decreased. The relationship is similar to that found for crustacean zooplankton in the Baltic Sea (Telesh et al. 2011). This intermediate salinity may represent a distinct physico-chemical barrier between marine and freshwater faunas due to changes in the ionic composition of the water, which then decreases the diversity of metazoan plankton (Khlebovich 1968).

### 5.2 Predation by Zooplanktivorous Fish: Is Selection Impaired by Turbidity? (II)

In the aquarium experiments investigating turbidity as an environmental deterrent of selective predation, the total prey consumption of sticklebacks decreased in elevated turbidity, consistent with other studies on vision-oriented particulate feeders (e.g. Nurminen et al. 2010, Estlander et al. 2012). In contrast, several earlier studies on sticklebacks feeding on larger benthic prey have indicated trivial or even nonexistent decreases in foraging success in higher turbidities, suggesting that sticklebacks may compensate for visual impairment by chemical cues (Quesenberry et al. 2007; Webster et al. 2007). However, our result emphasizes the view that zooplanktivory is more vulnerable to decreasing visibility than benthic feeding on larger and/or sessile prey (Horppila et al. 2010; Estlander et al. 2012).

Conversely, increased total prey consumption by roach in elevated turbidity was in line with a presumed
switch in feeding strategy, from particulate feeding to filter feeding, specifically to compensate for reduced visibility in turbid water (Lammens et al. 1987). This switch in feeding strategy has been observed in roach in reduced light conditions (Van den Berg et al. 1993). The significant increase in feeding in turbid water found in our experiments indeed implies a switch to an efficient filter feeding mode to maintain, or in this case increase, consumption. Similar conclusions have been drawn in a study by Nurminen et al. 2010. However, low total consumption by roach in the clear water control was problematic, as it may have been due to uncontrolled factors, such as predation risk or schooling behavior. It has been suggested that turbid environments may actually offer protection to juvenile fish from their predators (Gradall & Swenson 1982; Gregory & Northcote 1993; Lehtiniemi et al. 2005). An important factor affecting feeding motivation is predation risk (Reiriz et al. 1998), and juveniles used here may have found it too risky to feed actively in the clear water control. The decreased foraging activity subsequently resulted in reduced encounter rate with prey. Furthermore, the roach is a facultative schooling species which aggregates when foraging (Haberlehner 1988) and could be too intimidated to feed individually. Due to these uncertainties, the roach data were not included in paper II.

Selectivity patterns were similar for both predators in clear water, where the most highly consumed prey type was expectedly the large daphnid, as zooplankton body size is known to correlate with susceptibility to predation by zooplanktivorous fish due to factors related to preference or accessibility (Brooks & Dodson 1965; Kohler & Ney 1982). Cladocerans are more vulnerable than copepods because of inferior escape ability (e.g. Wong 1996; O’Keefe et al. 1998; Kiorboe et al. 1999). The positive selection for the daphnid by sticklebacks was consistent throughout the treatments, even though total prey consumption as well as specific consumption of daphnids decreased in highly turbid water. A similar pattern of increased or unaffected predation on larger prey types in diminished visual conditions has been detected in other vision-oriented feeders (Mikheev et al. 2004; Salonen & Engström-Öst 2010).

Out of the copepods Acartia was consumed at higher rates than Eurytemora by sticklebacks in clear water. Higher capture success rates per predator encounter have been recorded for Acartia, compared to Eurytemora (Viitasalo et al. 2001). In the turbid treatments this difference in consumption rates was imperceptible. An early escape response by Acartia may prevent encounters with predators in conditions where visual constraints impair prey detection, dampening the difference caused by genus-specific capture success rates (Viitasalo et al. 2001).

As expected, roach did not display similar strong selection for Daphnia. Notwithstanding the clear water control where Daphnia was positively selected, there was no statistically significant
selection for the different prey types. This has also been documented in previous studies on cyprinids (Mikheev et al. 2004; Estlander et al. 2010). The aggregating behavior and moderate swimming velocity of daphnids is expected to render them prey by default, and vulnerable to predation in large clusters by filter feeding. As previous studies using other filter-feeding fish have documented, these fish tend to be escape-selective rather than size-selective zooplankton predators, with a higher tendency to consume zooplankton with poor motility and inferior swimming ability regardless of size, and lower “preferences” for fast-swimming copepods (Drenner et al. 1982; Gophen et al. 1983; Persson 1987b). In terms of copepod selection, the higher consumption of *Eurytemora* compared to *Acartia* in the clear water control is consistent with escape-selective predation. *Acartia* is more stationary and ‘alert’, and theoretically more sensitive to the hydrodynamic disturbance created by cruising predators that approach at high speed (e.g. Viitasalo et al. 1998; Viitasalo et al. 2001). We did not quantify or record predator swimming behavior, but studies have shown that differential feeding behavior in selective and filter feeding fish (discontinuous searching, vigorous attacks and repeated strikes vs. continuous swimming and schooling) results in differences in prey capture efficiency, especially when foraging on evasive copepods (Peterka and Matěna 2011).

Many of the studies on the effects of turbidity on Baltic zooplanktivores have centered around algal turbidity, because of the topical interest in eutrophication (e.g. Lehtiniemi et al. 2005; Engström-Öst & Mattila 2008; Salonen et al. 2009; Ajemian et al. 2015). Yet inorganic clay is also considered a main component of turbidity in coastal areas (Mobley 1994), which is why our experiments were conducted using natural clayish sediment to simulate turbidity caused by the resuspension of bottom sediments. Climate change models predict that extreme weather phenomena in Europe will become more common during the course of this century (Beniston et al. 2007), which could lead to storm surges and coastal erosion increasing the amounts of inorganic suspended solids in the water column. Compared to algal turbidity, which can affect zooplanktivorous feeding at relatively low levels of ca. 5 – 7 NTU (Salonen & Engström-Öst 2010; Salonen & Engström-Öst 2013), inorganic turbidity was not found to affect feeding at correspondingly low levels. Both the size and the shape of the suspended particles influence the scattering and absorption of light in the water column (Kirk 1981), and identifying the source of turbidity is key in assessing effects on feeding. Our results confirm that inorganic turbidity, at the extreme levels that can occur in estuaries, can be detrimental to visually feeding zooplanktivorous fish, but the effects are not directly comparable to those caused by algal turbidity of equivalent NTU.
5.3 PREDATION BY ZOOPLANKTIVOROUS FISH: EFFECTS ON ZOOPLANKTON COMMUNITY (III)

5.3.1 COMMUNITY SIZE STRUCTURE AND TOTAL ABUNDANCE

Zooplankton community size structure can reflect the abundance of zooplanktivorous fish, the intensity of zooplanktivory, or both (Brooks & Dodson 1965). In our mesocosms, the structural development of a spring community initially dominated by rotifers was efficiently controlled by the predatory removal of large crustaceans. The differences observed in the two predators in aquarium experiments were emulated in the community-wide size structure: The intense predation by sticklebacks clearly decreased mean weighted size of the target prey population, while roach predation merely kept size from increasing. Large crustaceans were presumably the individually sought target prey of sticklebacks, whereas the overall low crustacean density was likely to encourage feeding on smaller prey by cruising roach. Prey availability and escape ability were more important than size in shaping the community in roach enclosures, and so average zooplankter size did not decrease. In the crustacean-dominated summer community overall predation effects were more obvious than in the spring. Instead of merely suppressing the development of the community towards larger body size, predation by both predator types actively decreased mean prey size, and resulted in clear abundance peaks of small species (Synchaeta, Keratella and nauplii). Therefore, smaller zooplankton groups benefited from the presence of fish. Our results corroborated previous ones, which suggest that total zooplankton abundance is related to mere predator presence, whereas community composition is more affected by predator type (Des Roches et al. 2013).

5.3.2 COMMUNITY COMPOSITION: TARGET PREY

Predator assemblages can be the defining factor of zooplankton community structure, with even more extensive effects than environmental factors, such as temperature (Meerhoff et al. 2007). The most obvious predation-related structuring mechanism is direct removal by consumption. In our mesocosms, predation effects that were apparently caused by direct prey removal included the low densities of the cladocerans Pleopsis polyphemoides in the spring and Eubosmina in the summer in predator enclosures. These expectedly inflicted a large part of the dissimilarity found between the predator enclosures and the control, since large crustacean zooplankton (e.g. Acartia and P. polyphemoides) are strongly top-down controlled (Horsted et al. 1988). Both roach and sticklebacks can target large cladocerans according to our aquarium experiments, hence the effect was not dependent on predator type. In addition, the replacement of Pleopsis with the larger Podon leuckartii was observed only in the control. The interactive effects of predation and resource
competition are generally thought to cause species replacement in seasonal succession. However, intense predation is considered to keep populations at densities where exploitative competition is not significant enough to cause such species replacement (Gliwicz and Pijanowska 1989). In an extensive study of zooplankton in a littoral area similar to that surrounding our mesocosms, Scheinin & Mattila (2010) also found *P. leuckartii* to be unique to a specific mesotrophic site, suggesting that it may require biotic conditions that are rarely met, for example low levels of zooplanktivory.

The effects of predation on copepods were less straightforward, and more dependent on predator type. Established copepod populations appeared to even benefit from selective visual predation, with intense nauplii production resulting in substantial cohorts of copepodites and adults in the summer experiments. Zooplanktivory targeted cladocerans over copepods (II), and was more efficient at controlling population increases of cladocerans when copepod populations were well-established. The main compositional difference in copepod densities between the two predators was observed as a change in the competitive interaction between the calanoid copepods *Eurytemora* and *Acartia*. *Eurytemora* benefits from its higher food ingestion rates and probable higher growth efficiency when food resources are adequate (Adrian et al. 1999), and it clearly dominated the spring control. However, stickleback foraging influenced the interplay between the copepods and decreased food web persistence by causing the near extinction of *Eurytemora* (McCann et al. 1998). *Eurytemora* is expected to be the preferred prey for particulate feeders because of its larger size, and egg-carrying females are often targeted by visual predators (Rajasilta & Vuorinen 1983), while *Acartia* is less conspicuous because of its smaller size and the females’ egg depositing behavior (Viitasalo et al. 2001). The stickleback-induced *Eurytemora* extinction was in line with the recent observation of high predation pressure eliminating the relevance of resource competition as a community-structuring factor, leaving predation alone to control the prey population (Nicolle et al. 2011). In the roach enclosures *Acartia* also became the more abundant copepod by the final sampling, but without *Eurytemora* extinction. This was consistent with results from the aquarium experiments (II): Predation by cruising feeders does not target *Eurytemora* as such, but the ‘alertness’ of *Acartia* (Viitasalo et al. 2001) may result in lower predator encounter rate, rendering it less vulnerable to filter-feeding roach. In general, predators are expected to promote diversity when their impact is greater, but not eliminative, on the dominant competing prey. Through this mechanism, roach predation maintained prey diversity, which was depicted by the relatively stable *FD* values.

However, in the summer experiments the interaction was altered due to the initial community structure and lower phytoplankton availability. In direct reversal to the spring experiment,
Acartia was clearly more abundant than Eurytemora in the control enclosures. The lower phytoplankton availability of the summer period conceivably favored Acartia, which has a wider food niche resulting from its unique capacity for raptorial as well as suspension feeding (Gyllenberg 1980; Tiselius 1990; Adrian et al. 1999). It is reasonable to assume that increased resources in the form of rotifers and nauplii buffered predation effects on Acartia.

Stickleback predation enhanced the difference in relative calanoid abundances, since Eurytemora is more susceptible to selective predation. Predation efficiency on Acartia was presumably higher in the roach enclosures, resulting in a lower abundance of Acartia compared to the stickleback enclosures. This could be evidence of a switch in the roach feeding strategy in the summer period. Theoretically, large body size of the average prey encourages particulate feeding in a zooplanktivore that is capable of both strategies (Lammens 1985; Lammens et al. 1987). This was supported by the altogether minimal differences between the predator enclosures in the summer period, as well as the effective decline in size structure in roach enclosures, which was a conceivable indication of size-selective feeding.

Clearly, the Acartia/Eurytemora interaction indicates that predation experiments in confined aquarium areas may not be directly applicable to more natural full-community circumstances. Contrary to what would be expected from the result of the aquarium experiments, where Acartia was positively selected by sticklebacks, predation appeared to affect Eurytemora more severely than Acartia in the mesocosms. This could be due to complicated indirect effects of resource competition induced by predation, or alternatively the lack of spatial constraints in comparatively natural surroundings, allowing the evasive strategy of Acartia to prevent it from being detected and consumed. The specific preference for Acartia by selective zooplanktivory could be construed as an artefact of the experimental setup, although we cannot be sure of the exact mechanism (direct removal vs indirect effects) causing the Eurytemora population decline in the mesocosms.

5.3.3 COMMUNITY COMPOSITION: CASCADING EFFECTS

Predation does not merely affect target prey, but can have community-wide effects due to trophic cascades, changes in competitive inter-species interactions and anti-predator behavior in prey organisms (Eklöv & VanKooten 2001; Englund 2005). Much of the variation induced by predation in our mesocosm experiments was credited to a few key taxa, some of which were components of microzooplankton, and not direct target prey of either predator. Several microzooplankton groups (T. lobiancoi in the spring and calanoid nauplii in the summer) underwent a rapid population surge in the predator enclosures, while rotifers followed enhanced succession, undergoing either a crash (Synchaeta
in the spring) or an abrupt rise (K. quadrata in the summer). In control enclosures in the absence of predation, microzooplankton densities were much lower, and presumably limited by either resource competition or direct grazing by mesozooplankton (Kivi et al. 1993). Heterotrophic protists, such as ciliates, are subject to the same grazing pressure by mesozooplankton as similarly sized and shaped phytoplankton, and in the case of copepods, they are often the preferred prey item (Paffenhöfer et al. 2005; Vargas et al. 2006). Therefore, heterotrophic protists and other organisms at the base of the food web, with the exception of relatively impervious armored dinoflagellates, are usually kept in check by grazing, unless fish predation in turn impedes mesozooplankton, as was the case in the predator enclosures (Sanders & Wickham 1993; Jürgens et al. 1996; Johansson et al. 2004). Microzooplankton can contribute largely to total grazing, often consuming more than 50% of primary production (Calbet & Landry 2004), which could explain why the predatory removal of mesozooplankton grazers was not reflected in significantly higher phytoplankton biomass compared to control enclosures.

Predator enclosures generally had higher rotifer densities than the control during both experimental periods. Herbivorous cladocerans are known to suppress rotifers through mechanical interference or exploitative competition, especially species of Synchaeta, Keratella and Trichocerca (Gilbert 1989). As expected, rotifers in the predator enclosures underwent enhanced succession in the absence of large cladocerans and other crustaceans, such as the large omnivorous copepods, which readily ingest rotifers. Since fish predation removed larger competitors and potential predators, rotifers rapidly populated the newly produced vacant niches due to their fast reproductive rates (Likens 2010). The appearance of Keratella cruciformis in the spring and the shift from Synchaeta to Keratella in the summer were indications of rapid rotifer succession, as Keratella tends to succeed the more aggressively feeding raptorial Synchaeta in Baltic Sea coastal systems (e.g. Scheinin & Mattila 2010). Meanwhile abundances of Synchaeta and Keratella remained low in control enclosures, where they were presumably kept in check by large crustaceans.

5.3.4 COMMUNITY DIVERSITY

The initial composition of zooplankton community (i.e. seasonal variation) determined the degree of predation effects on diversity (III). In an initially diverse summer community the predation effect was not significant, whereas in a species-poor spring community, predation by sticklebacks significantly depleted diversity. In the spring, the stickleback enclosures became dominated by rotifers and the tintinnid T. lobiancoi, which indicated high predation pressure on mesozooplankton. Both taxonomic and functional diversity decreased in the stickleback enclosures in the spring period, and increased ($H'$) or remained the same ($FD$) in the roach enclosures. Initial diversity in the spring community was
low, and stickleback predation merely removed species and further depleted diversity. The collapse of functional diversity in stickleback enclosures in the spring reflects diversity on direct target prey. The collapse resulted from the loss of entire functional groups through predation, including groups consisting of cyclopoids, cladocerans and herbivorous copepods. The disappearance of these groups have strong implications on grazing processes, as well as the control of rotifer populations through direct consumption (cyclopoids) and resource competition (cladocerans) (Gilbert 1989; Nagata & Hanazato 2006). The decrease in taxonomic diversity reflected community-wide diversity, including non-target lower trophic levels, and was apparent before any significant decline in functional diversity. Typically species can be removed without obvious decline in ecosystem functioning due to a degree of functional redundancy, but once an entire functionally similar group expires, the collapse can be dramatic (Woodward 2009). However, in our mesocosms this removal of grazers was not reflected in a significant increase in phytoplankton biomass, possibly due to compensatory grazing by microzooplankton. Conversely to stickleback effects, predation by the cruising roach did not cause near extinctions of large crustaceans or intense domination by small plankters, so even with prey depletion, the functional composition of the prey community remained similar to the control.

In the more diverse summer community there were no effects on diversity by either predator. Diversity itself is a predation-regulating factor, because non-target prey cause weakened predator-prey interactions by masking prey, diluting prey concentrations, and/or confusing predators (Kratina et al. 2007). In addition, predation on a diverse cladoceran community likely weakened the link between predators and the less vulnerable copepods, which were allowed to stabilize their populations. Large and diverse cladoceran prey populations are less likely to be severely affected by moderate predation, because of their fast reproductive rates. Overall, the predation effect was coupled with temporal patterns of seasonality, so that high zooplankton diversity in the summer mitigated zooplanktivore control of the prey community, regardless of predator type. Similarly, high prey diversity has been shown to moderate the effects of top-down control of grazers on phytoplankton (Hillebrand & Cardinale 2004).

5.4 ZOOPLANKTON AS CONSUMERS: COPEPOD NAUPLIUS FEEDING ECOLOGY (IV)

The type, quality and amount of phytoplankton consumed by grazing zooplankton have immense consequences on the survival and reproduction of grazers in both freshwater (Ahlgren 1993; Müller-Navarra 1995; Repka 1997) and marine systems (Jonasdottir 1995; Turner & Tester 1997; Sopanen et al. 2006; Vargas et al. 2006). High-quality food sources are critical in maintaining growth and reproduction in
both zooplankton and their predators. It follows that the trophic transfer of food quality indicators, such as essential fatty acids, from primary producers to consumers, is the focus of a myriad of studies (e.g. Müller-Navarra et al. 2000; Brett et al. 2006; Persson & Vrede 2006). Copepod nauplii are a part of aquatic food webs as important prey for fish larvae (Siefert 1972; Munk & Kiorboe 1985); therefore understanding their feeding ecology is a crucial aspect of unraveling aquatic food web processes.

In this study, the functional responses of Paracartia grani for various microalgae represented either a type II or type III response, depending on prey type. The responses were relatively similar in terms of ingestion rate, but in terms of clearance rate, type III responses indicated a feeding threshold prey concentration, under which feeding decreased or ceased completely, in order to conserve energy (Price & Paffenhofer 1985). When the prey concentration and subsequent energy gain was not high enough to compensate for energy loss through the predation process, P. grani nauplii demonstrated very low clearance rates. This was found in all prey except the optimal prey types Heterocapsa sp. and Thalassiosira weissflogii. Type III responses have recently been identified in copepod nauplii (e.g. Almeda et al. 2010), and may be more common than previously thought in zooplankton (Sarnelle & Wilson 2008). They have generally not been taken into consideration because of a lack of empirical observations at low food levels. Yet the type III response may be a significant ecosystem stabilizing mechanism, as it reduces prey mortality when prey populations are low in density, and therefore potentially vulnerable to extinction (Murdoch 1969; Roughgarden & Feldman 1975).

As expected for nauplii of the size of Paracartia grani, the dinoflagellate Heterocapsa sp. and the diatom T. weissflogii represented optimum prey in terms of size (Berggreen et al. 1988). The daily rations obtained from different prey types varied to a great extent, suggesting that factors of palatability and prey morphology result in satiation levels at differing levels of energy input. For example, prey types can vary in the extent to which they fill the nauplius gut due to different shapes and outer structures. In general, satiation was achieved at a prey concentration of 200 – 500 ng C ml⁻¹. This could be regarded as the energy requirement for P. grani nauplii in non-limiting prey conditions.

In grazers, the concept of switches in prey preference with prey availability may have powerful implications for phytoplankton succession and competition. However, in this study nauplius clearance rates remained relatively constant in the plurialgal mixtures, regardless of the concentrations of prey types, with high clearance rates for dinoflagellates. The only exception to this was the low clearance of Heterocapsa sp. in the presence of low concentrations of I. galbana. Further experimentation and actual microscopic observation of feeding behavior may reveal the mechanism behind this result, but it may be related to complicated interactions between the
prey types themselves, which potentially increase encounter rate between predator and prey (*Heterocapsa* sp.) at higher concentrations of a less targeted prey (*I. galbana*). This study emphasizes the need for more experimentation on plurialgal mixtures, which resemble natural systems. The presence of several prey types undoubtedly complicates feeding relationships because of prey selectivity and the added interactions between prey, and may result in paradoxical observations.

Although *P. grani* does not occur in the Baltic Sea, the closely related *Acartia* is a cosmopolitan genus, and results obtained in this study can be incorporated to model Baltic ecosystem functioning as well. *Acartia* is often the dominant calanoid copepod in Baltic coastal waters, and in the central Baltic Sea it has been thought to have benefited from the recent trend of increasing water temperature and decreasing salinity (Möllmann et al. 2005). However, a recent long-term study has indicated the exact opposite pattern in the open sea areas of the Gulf of Finland, where increasing temperature was related to *Acartia* population decline (Suikkanen et al. 2013). A simultaneous shift in phytoplankton community composition from Cryptophyceae, which is considered high-quality food for zooplankton (Lehman & Sandgren 1985), to phytoplankton classes that are an inferior food source, may also partially explain the decrease in *Acartia* abundance (Ljunggren et al. 2010; Suikkanen et al. 2013).

The prevalence of calanoid nauplii in the field sampling of this study (I), as well as their significance as a resource component in the interactions between zooplankton and zooplanktivorous predators (III), indicate that their trophic role in the coastal Baltic Sea may be more extensive than previously conceived. Moreover, the population-age structure hypothesis predicts that warming waters, such as those of the coastal Baltic, present a competitive advantage to younger and smaller age classes by increasing their metabolism (Daufresne et al. 2008; Ohlberger et al. 2011), thereby potentially changing population structure. This could emphasize the role of nauplii as grazers in the Baltic Sea ecosystem. In essence, functional response experiments can be a useful way to quantify nauplius feeding requirements and subsequent grazing potential, especially in response to phytoplankton dynamics. The resulting data can be used as direct inputs in food web models.
6. CONCLUSIONS AND FURTHER STUDIES

Total zooplankton abundance was consistently found to be related to temporal variation (I, III), and it directly reflected the size structure of the community in the natural ecosystem and in the mesocosms. Salinity was a major regulating force of zooplankton community composition, as it is to communities of other Baltic Sea organisms (Ojaveer et al. 2010), so drastic changes in salinity can be expected to have major consequences for coastal zooplankton biodiversity. The experimental results seemed to parallel observations in the field, confirming the relevance of the predation experiments. Zooplankton abundance was found to be relatively similar in nature and the experimental mesocosm communities in the presence of predation, and additionally comparable with a recent study conducted in ecologically similar areas in the Baltic Sea (Scheinin & Mattila 2010). The late summer rotifer abundance peak that occurred in predator enclosures in mesocosm experiments is also observed in the natural Baltic Sea system (I), suggesting that predation effects in the experimental mesocosms were at least partially comparable to those in real ecosystems.

Zooplanktivores consume prey according to their physiological needs and capabilities, and control community structure of zooplankton through their feeding behavior. By doing so, they can eventually have significant impacts on ecosystem effects through factors such as phytoplankton control by grazing. This study emphasized the subtle cascading effects of zooplanktivorous fish on microzooplankton components of the food web (III). Moreover, interesting implications arise from our experiments on the deleterious effects of turbidity on zooplanktivory (II). Three-spined sticklebacks in the Baltic Sea have been presumed to benefit from climate change, because of higher feeding rates related to increasing temperature (Lefèbure et al. 2014), coupled with a simultaneous decline in coastal piscivores (Ljunggren et al. 2010). However, even if zooplankton resource levels remain high, significant increases in turbidity caused by climate change-related phenomena, such as eutrophication and erosion, could affect stickleback populations if feeding efficiency decreases to the extent detected in our feeding experiments. Nevertheless, despite reportedly high turbidity values in coastal zones, the turbidity levels measured in littoral sampling sites in this study (I) were not currently high enough to impede feeding to the extent that was observed in the aquarium experiments (II). Whether these results can be applied to community-wide effects is ambiguous without further large-scale experimentation in turbid conditions, as well as experiments combining multiple environmental stressors. However, there is an implication that an environmental change affecting only specific predators has the potential to mitigate top-down control, while the role of unaffected predators may become accentuated.

Inspecting zooplankton using trait-based approaches is becoming more
commonplace, because groupings based on function, rather than taxonomy, are especially useful for studies on food web processes. This study utilized traits that are a direct indicator of interaction through equivalent diets. Nevertheless, functional classification was based largely on the degree of omnivory, rather than specific feeding patterns. To enable a more detailed functional classification of zooplankton based on resource use traits, further species-specific feeding experiments quantifying functional responses are necessary. Future studies should also include functional response types using traits such as generation time, reproductive rate, body size, escape ability and swimming velocity. These could provide indications of community stability and resilience, by quantifying the recovery potential of zooplankton as prey populations.

This thesis adds details to knowledge of the trophic ecology of littoral zooplankton. The main focus has been the abiotic and biotic factors that affect zooplankton community composition and diversity. Because of the strong community-structuring roles of abiotic factors such as salinity and turbidity, as well as biotic factors such as predation, littoral zooplankton communities will undoubtedly be significantly altered along with the changes associated with the forthcoming regime shifts occurring with climate change.
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