Patterns and processes of littoral zooplankton composition in relation to the trophic state of the environment

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"Mitä epämukavampaa, sitä mukavampaa."
-Eero O. Kasanen-

Abstract

This thesis is about bidirectional interplay between patterns and processes of community composition under varying environmental conditions. Each of the four papers that form the basis of the thesis views the research theme through its own theoretical or conceptual framework. The primary purpose of the thesis is to develop those frameworks. They are interrelated via the study system, communities in flads (i.e. lagoon-like inlets) representing contrasting trophic and alternative community states in the northern Baltic Sea. A further goal of this thesis is thus to increase understanding of the study system.

In the four papers of the thesis, patterns and processes of community composition are reflected principally through zooplankton. The papers constitute a continuum from describing patterns towards explaining processes behind them. The first two papers relate patterns of zooplankton composition (Paper I) and the state of the ambient community (Paper II) to the trophic state of the environment. Zooplankton was sampled in two flads in low and in two flads in high trophic states over an entire growth season to encapsulate much of the landscape-level and seasonal variation in patterns of littoral zooplankton composition in the northern Baltic and to relate the patterns to productivity, in general. The compositional patterns were viewed from a functional perspective, with the focus on the abundance and α-diversity of zooplankton. The four flads were revisited during another growth season to evaluate and reflect the state of the associated communities through planktic microalgae and macrophytes. The extent of variation in the composition of these primary producers was assessed at both local (within flads) and landscape-level (among flads) spatial scales, and at different i.e. diurnal (over a day) and seasonal (over a growth season) temporal scales. The last two papers focus on how processes of zooplankton composition are affected by qualitative (Paper III) and quantitative (Paper IV) changes in community state in various scenarios associated with the trophic state of the environment. The assemblage and/or relative densities of different foundation species, core zooplanktivores and keystone piscivores were manipulated in mesocosms to reflect consequent short-term (from half an hour to a day) changes in zooplankton populations and communities among habitats varying in their physical structure (i.e. their structural complexity) formed by foundation species. The experiments thus addressed processes of zooplankton composition at habitat (within habitats) and local (among habitats) spatial scales and at the diurnal temporal scale. The structuring role of habitat complexity on these scales was also assessed over a whole growth season in each of the four study flads representing contrasting trophic and alternative community states.

The patterns of zoo- and microalgal plankton composition varied in distinct manners with the trophic and community states of the flads. This landscape-level variation decreased towards the end of the growth season, in conjunction with the variation in the trophic and in contrast with the variation in the vegetative (community) state of the flads. The magnitude of local and diurnal differences in zoo- and microalgal plankton composition increased with the trophic and varied with the community state of the flads. This small-scale variation was generally low at both ends of the growth season. Furthermore, the composition of zooplankton varied locally and diurnally considerably more than that of microalgal plankton, suggesting that the habitat complexity formed by foundation species is not associated with zooplankton composition through microalgal plankton. The manipulative experiments clarified how the structuring role of habitat complexity can be associated with zooplankton composition. First, the structuring role of habitat complexity varied within the zooplankton. Similar environmental conditions were reflected differently in the various zooplankton groups. Some were concentrated in the open water, others in the foundation species, whilst still others were evenly distributed between those habitat types. Second, the structuring role of habitat complexity varied depending on qualitative community changes associated with the trophic state of the environment. Different foundation species, core zooplanktivores and keystone piscivores and complex interactions among these community components altered the way zooplankton was distributed among habitats with contrasting complexity. Third, these impacts varied depending on the environmental context such as the time of day. In addition to their assemblage, the relative densities of foundation species, zooplankton and core zooplanktivores exerted fundamental impacts on the structuring role of habitat complexity in zooplanktivory, a central process of zooplankton composition. In a community state scenario where the densities of foundation species increased, while those of zooplankton and core zooplanktivores remained constant, zooplanktivory decreased with increasing habitat complexity. In contrast, this protective relationship did not exist in a scenario where the densities of the three components increased in parallel, as often happens when the trophic state of the environment increases. Instead, zooplanktivory was determined explicitly by the aggregate density of zooplankton and zooplanktivores, indicating that the impacts of foundation species on the ambient animal community differ in their type and magnitude depending on the trophic position of the animals and their environmental context.

In summary, patterns and processes of littoral zooplankton composition change interdependently with each other and with the trophic state of the environment. The relative importance of bottom-up regulation seems to decrease and that of top-down regulation to increase together with spatial and temporal scales. Instead of being a trophic component, macroscopic primary producers seem to be intimately involved in both bottom-up and top-down processes determining community composition on several scales by contributing to the physical structure of the environment. The density and diversity of foundation species and thus the concept of habitat complexity is essential for understanding the structure and functioning of littoral environments in general.

The two central concepts on which the thesis work was built upon proved to be essential for understanding observations from the study system in the light of ecological theory. First, ecological processes not only generate ecological patterns but also depend on them. Since patterns affect each other through processes and processes affect each other through patterns, basically any alteration in either of these has cascading consequences. Second, ecological patterns and the underlying processes can occur on different spatial, temporal and organizational scales. Observed patterns may emerge collectively from large ensembles of smaller-scale units or be imposed by larger-scale constraints. Understanding patterns on one scale thus involves studying processes on others and vice versa. Since patterns and processes are integrally intertwined, one cannot be understood without the other.

Sammanfattning (abstract in Swedish)

Denna avhandling handlar om hur samhällskomposition och dess reglering påverkar varandra under varierande omgivningsförhållanden. Var och en av de fyra delarbeten som utgör denna avhandling betraktar forskningstemat genom sina egna teoriramar och begreppsapparater. Avhandlingens primära målsättning är att utveckla dessa teoriramar. De sammankopplas av studiesystemet d.v.s. samhällen i norra Östersjöns flador (lagunlika, små vikar), som representerar kontrasterande trofiska nivåer och samhällen i alternativa tillstånd. Således är avhandlingens sekundära målsättning att öka kunskap om studiesystemet.

I de fyra delarbetena betraktas samhällskompositionen huvudsakligen genom djurplankton. Syftet hos delarbetena utvecklar sig från att beskriva samhällsmönster mot att förklara hur de uppstår. De två första delarbetena länkar samhällsmönster hos djurplankton (Paper I) och tillståndet hos det omgivande samhället (Paper II) till omgivningens trofiska nivå. Djurplanktonprov togs i två flador med låg och i två flador med hög trofisk nivå över en hel tillväxtsäsong. Detta gjordes för att täcka så mycket som möjligt av landskaps- och säsongsvariation i samhällsmönstren hos litoralt djurplankton i norra Östersjön och för att koppla dessa mönster till biologisk produktivitet. Samhällsmönstren betraktades ur en funktionell synvinkel med betoning på djurplanktons mängd och α-diversitet. De fyra fladorna återbesöktes under en annan tillväxtsäsong för att utvärdera och avspegla tillståndet hos organismsamhällena i fladorna genom planktonalger och makrofyter. Variationsbredden i dessa primärproducenters komposition avgjordes på lokal (inne i fladorna) och landskapsnivå (mellan fladorna) samt på dygns- (över ett dygn) och säsongsnivåer (över en tillväxtsäsong). De två sista delarbetena är fokuserade på hur processer som styr djurplanktonkomposition påverkas av kvalitativa (Paper III) och kvantitativa (Paper IV) förändringar i det omgivande samhällets tillstånd. Dessa förändringar avspeglade potentiella scenarier relaterade till variation i omgivningens trofiska nivå. Sammansättningen och/eller de relativa tätheterna hos olika fundament- (makrofyter), kärn- (djurplanktonätare) och nyckelarter (fiskätare) manipulerades i mesokosmer för att utreda hurdan kortsiktig (från en halv timmes till ett dygns) inverkan dessa förändringar hade på djurplanktonpopulationer och -samhällen beroende på habitatets strukturella komplexitet (utgjord av fundamentarterna). Således var mesokosmförsöken inriktade på processer som styr djurplanktonkomposition på habitat-, lokal och dygnsnivåer. Habitatkomplexitetens strukturerande roll på dessa skalor avgjordes även över en hel tillväxtsäsong (på säsongsskala) i de fyra undersökningsfladorna.

Mönster i djurplankton- och planktonalgkomposition samvarierade på ett säreget sätt med fladornas trofiska nivå och med tillståndet hos samhällen i dem. Denna variation på landskapsnivå minskade mot slutet av tillväxtsäsongen i likhet med variationen i fladornas närsaltshalter, medan tillståndet hos (makrofyt)samhällena utvecklade sig på motsatt sätt. Omfattningen hos lokal och dygnsvariation i djur- och planktonalgkomposition ökade tillsammans med fladornas trofiska nivå, varierade med tillståndet hos samhällen i dem och var generellt liten i båda ändorna av tillväxtsäsongen. Därtill var lokal och dygnsvariationen mycket högre hos djurplankton än hos planktonalger. Detta tyder på att planktonalgerna inte var en viktig faktor för sambandet mellan djurplanktonkomposition och den habitatkomplexitet som utgjordes av fundamentarter. Mesokosmförsöken klargjorde hur habitatkomplexitetens strukturerande roll är länkad till djurplankton. För det första varierade denna roll inom djurplankton. Olika djurplanktongrupper reflekterade likadana omgivningsförhållanden på olika sätt. Somliga var koncentrerade i öppet vatten och andra inne i fundamentartsbestånd. Därtill var många grupper jämnt utspridda mellan dessa habitattyper. För det andra varierade habitatkomplexitetens strukturerande roll beroende på kvalitativa samhällsförändringar som typiskt är anknutna med omgivningens trofiska nivå. Olika fundament-, kärn- och nyckelarter (makrofyter, planktonätande fiskar och fiskätande fiskar) och olika typer av växelverkan mellan dem påverkade djurplanktonutbredningen bland habitat med olika strukturell komplexitet. För det tredje varierade dessa påverkningar beroende på yttre omgivningsförhållanden såsom tiden på dygnet. Utöver sammansättningen hos fundament-, kärn- och nyckelarter hade de relativa tätheterna hos dem en grundläggande inverkan på habitatkomplexitetens roll i predation på djurplankton – en av de mest centrala processer som styr kompositionen hos djurplankton. I ett scenario där tätheten hos fundamentarter ökade medan tätheten hos djurplankton och (djurplanktonätande) fiskar hölls på samma nivå, minskade predation på djurplankton med ökad habitatkomplexitet. Däremot förekom inget dylikt skyddsförhållande i ett scenario där tätheterna hos alla tre samhällskomponenter samvarierade – som ofta är fallet när omgivningens trofiska nivå förändras. Istället bestämdes predationseffektiviteten allenast av den sammanlagda tätheten hos båda djurgrupperna. Dessa

iakttagelser tyder på att fundamentarternas inverkan på det omgivande djursamhället varierar i sin typ och omfattning beroende på djurens trofiska position och deras övriga icke-levande och levande miljö.

Sammanfattningsvis kan konstateras att förändringar i kompositionsmönster hos litoralt djurplankton och i processer som reglerar dessa mönster är beroende av varandra och omgivningens trofiska nivå. Den relativa betydelsen för djurplanktonkomposition som växelverkan med lägre trofinivåer har, verkar öka med växande rumsliga och tidsliga skalor. Däremot verkar den relativa betydelsen hos växelverkan mellan djurplankton och högre trofinivåer minska. Istället för att vara bara trofiska komponenter verkar makroskopiska primärproducenter, genom att bidra till omgivningens strukturella komplexitet, vara djupt inrotade i både resurs- och predationsbaserade processer som styr samhällskomposition på flera skalor. För att kunna förstå strukturen och funktionen hos litorala miljöer i allmänhet är det nödvändigt att ta i beaktande tätheten och diversiteten hos fundamentarter.

De två centrala idéer som avhandlingsarbetet var byggt på visade sig vara essentiella för att koppla ihop iakttagelser från studiesystemet och ekologisk teori. För det första ger ekologiska processer inte bara upphov till naturens mönster utan beror även på dem. För att mönster påverkar varandra genom processer och för att processer påverkar varandra genom mönster, har i princip vilken förändring som helst i någotdera kaskadaktiga följder. För det andra förekommer mönster i naturen och processer bakom dem på flera rumsliga, tidsliga och organisatoriska skalor. Iakttagna mönster kan uppstå kollektivt från stora ansamlingar av enheter på mindre skalor eller vara bestämda av begränsningar på större skalor. Att förstå mönster på en skala innebär således att undersöka processer på andra skalor eller tvärtom. Eftersom mönster och processer är oskiljaktiga, är det omöjligt att förstå det ena utan det andra.

Contents

List of original papers

This thesis is based on the following Papers, which will be referred to in the text by their Roman numerals.

Paper I
Scheinin M, Mattila J. 2010. The structure and dynamics of zooplankton communities in shallow bays in the northern Baltic Sea during a single growing season. Boreal Env Res 15: 397-412.

Paper II
Scheinin M, Sjöqvist C, Mattila J. Microalgal plankton composition in shallow coastal inlets in contrasting trophic and alternative community states. Manuscript accepted for publication in Hydrobiologia.

Paper III
Scheinin M, Mattila J. Habitat complexity interconnects patterns and processes of community composition. Manuscript.

Paper IV
Scheinin M, Scyphers SB, Kauppi L, Heck KL, Mattila J. 2011. The relationship between vegetation density and its protective value depends on the densities and traits of prey and predators. Oikos 121: 1093-1102.

1 Introduction

Ecological processes not only generate but also are dependent upon patterns (Schröder and Seppelt 2006). Since patterns affect each other through processes and processes affect each other through patterns, basically any alteration in one will have cascading consequences. Because patterns and processes are integrally intertwined, one can not be understood without the other (e.g. von Bertalanffy 1950).

This thesis is concerned with the interplay between patterns and processes of community composition. Communities change with their environment. These changes are typically associated with abiotic factors that promote biological productivity (e.g. Lindeman 1942). Alterations in e.g. nutrient availability affect the complex nexus of processes among the abiotic and biotic components of natural systems. Consequently, the components of the system change and/or vary in their levels. It is these qualitative and quantitative alterations that determine the interplay among the components and are thus reflected back in processes of community composition. Processes that are important for structuring a system change with its components and can involve both bottom-up and top-down regulation regardless of the ultimate driver (Jeppesen et al. 2000). Unraveling the principles of how communities change with their environment rests thus on two fundamental premises. The first one is to detect and describe patterns of community composition in relation to the environment. The second and the more demanding one is to identify and quantify the processes that are responsible for those patterns.

The purpose of this thesis is to increase understanding on how patterns and processes of community composition change with the trophic state of the environment. The study system builds upon communities in lagoon-like inlets, or "flads" (Ingmar 1975, Munsterhjelm 1997, 2005) that represent a landscape-level trophic gradient in the northern Baltic Sea. In the four papers that constitute the basis of this thesis, patterns and processes of community composition are reflected principally through zooplankton (see Paper I for definition). The first two papers relate patterns of zooplankton composition (Paper I) and the state of the ambient community (Paper II) to the trophic state of the environment. The last two papers focus on how processes of zooplankton composition are affected by the qualitative (Paper III) and quantitative (Paper IV) changes in the ambient community.

Each of the four papers views the research theme through its own theoretical framework and associated concepts. Paper I is concentrated on the relationship between zooplankton α-diversity and the trophic state of the environment (e.g. Johansson 1992, Attayde and Bozelli 1998, Jeppesen et al. 2000, Barnett and Beisner 2007) and introduces (and renounces) the Biodiversity and Ecosystem Function (BEF) framework (Walker 1992, Schultze and Mooney 1993). In Papers II and III the focus is broadened from the α-diversity to the overall composition of zooplankton and from the trophic to community state of the ambient environment. Accordingly, β-diversity as such (Whittaker 1960) and more process-oriented or functional facets such as the

trophic (Lindeman 1942) and size structures (Hutchinson 1959, Hutchinson and MacArthur 1959) of communities are related to nutrient levels and associated environmental conditions. In this context, also the theoretical framework around alternative stable states (Lewontin 1969, Holling 1973, May 1977) and the concepts of foundation (Dayton 1972), keystone (Paine 1966, 1969) and core species (Hanski 1982) are introduced. Additionally, Paper III introduces the concept of habitat complexity and the associated theoretical framework (Klopfer and MacArthur 1960, MacArthur and MacArthur 1961, Simpson 1964). Paper IV builds specifically on that framework, with particular focus on the quantitative aspects of habitat complexity.

Theoretical frameworks have been introduced, rejected and modified as ecological theory and observations from the study system have provided mutual guidance and refinement. The thesis summary presents an eclectic and overarching perspective on the study system and thus on principles of community composition. Instead of being a snapshot, this summary depicts the progression to the present perspective and predicts how the interplay between ecological theory and observations on the study system will mutually develop in the future. The concepts and theoretical frameworks that are relevant for the present, overarching perspective on the research topic are thoroughly reviewed in the introduction of the summary. This is followed by a comprehensive account on the study system. This kind of unambiguity is especially important in community ecology, as it constitutes the interface between population and systems ecology, disciplines differing fundamentally in some of their conventions.

1.1 Concepts and approaches

1.1.1 Defining communities

A community is an association of species co-existing in a given space. This definition is open to various interpretations. Firstly, a community may refer to the entire biota or some of its compartments in the given space. For instance, zooplankton communities are functionally and plant communities taxonomically defined compartments of larger associations of organisms. Furthermore, the boundaries of the space that a community occupies are more or less arbitrary. A lake, for example, may be a relatively clearly demarcated space. In contrast, the same is not true for the pelagial of the lake. As a hierarchical scale of biological organization (see 1.1.3), a community or a biocoenosis is an interspecific grouping of populations, which together with its physical environment forms an ecosystem (Begon et al. 2008). In practice, communities are often associations of organisms occurring in samples supposed to represent a given space, in this thesis, a flad.

1.1.2 Assessing composition

Patterns of composition refer to the identities and relative abundances of organisms in an association

such as a community. Although these qualitative and quantitative aspects are inseparable, distinguishing between them simplifies the interpretation of compositional patterns. The qualitative aspects are expressed e.g. as the species, functional groups, ontogenetic stages and size classes present in an association of organisms. The quantitative aspects simply refer to the abundances of those units and are denoted e.g. as numbers, densities, biomasses and carbon contents.

Processes of composition refer to the interplay among organisms and their environment. In addition to the association of organisms, those processes include and thus compose even the non-living environment. Compositional processes can be categorized as endo- (internal) or exogenous (external) (Bolliger et al. 2005). The categorization depends on the scale of observation (Paper III). For a community, for instance, processes such as predation and competition would be endogenous. In contrast, processes like eutrophication and rainfall would be exogenous. Furthermore, interactions among organisms and their environment lead to two types of compositional alterations. Turnover refers to the natality and mortality of organisms and migration to their immigration and emigration (Paper III). These basic compositional processes add up to larger ones, such as speciation and extinction.

To understand patterns and processes of composition together, communities or other associations of organisms can be viewed via their functional properties. Various metrics can be applied in conjunction with the compositional information to quantify the structure of associations. Some metrics only summarize and simplify the compositional information, whilst others may incorporate additional information. For example, if the information regards species and their abundances, total abundance can reflect the quantitative and species richness the qualitative information, whilst α-diversity can sum up both types of information (Paper I). In contrast, metrics such as size structure and trophic structure are based on the sizes and trophic positions of the species, i.e. on information that is supplemental in this case (Papers II and III). Both types of structural metrics may reveal a great deal about the processes that generate and depend on the compositional patterns. For instance, the size structure of zooplankton can reflect the abundance of zooplanktivorous fish (i.e. patterns), the magnitude of zooplanktivory (i.e. processes) or both (Brooks and Dodson 1965, Paper III).

1.1.3 Demarcating scales

Spatial and temporal scales are, in addition to the organizational ones, arbitrary but convenient divisions for interpreting ecological patterns and processes. The relevance of different patterns and processes changes gradually along each type of scale. In general, the importance of biotic patterns and processes decreases whereas that of abiotic ones increases with increasing scale (Hutchinson 1953, Levin 1992). Nonetheless, patterns and processes are interdependent across all scales, either directly or indirectly.

Similar to organizational and temporal scales, also spatial scales are divided hierarchically. However, the associated terminology is inconsistent and the demarcation case-specific or purpose-oriented. A physical habitat, i.e. the environment where an organism or ecological community normally occurs under given circumstances, is a convenient basis for the spatial hierarchy. Conventionally, habitats add up to localities, localities to landscapes and landscapes to regions. In this thesis, the northern Baltic is viewed as a region, the archipelago of Åland Islands as a landscape, the study flads as localities and structurally uniform stands of macrophytes as habitats (Papers I, II and III). The central spatial scale in this thesis, the landscape scale, is the interface between the biotic and abiotic processes that compose communities. A landscape can be seen as a pool of organisms with potential to occur in any local-scale entity within the landscape. Factors that are exogenous and thus more or less equal for the entire landscape lay the foundations and boundaries for the pool. Within the landscape, the composition of local associations of organisms often co-varies with abiotic factors such as salinity or the degree of isolation. Apart from getting disrupted by each other, such correlative relationships can be obscured by strong biotic interactions. Organisms involved in such interactions are central for the structuring and functioning of the system and are accordingly referred to as e.g. foundation, core and keystone species (see chapter 1.3.1 and Paper III).

The hierarchical division of temporal scales is clearer than that of the spatial scales. Important scales such as those related to the circular rhythmics in nature, e.g. days and years, are unambiguously defined. Other relevant scales such as growing seasons may vary more in their length but are still clearly defined. This thesis is focused especially on seasonal (Papers I, II and III) and diurnal scales (Paper II and III).

In addition to spatial and temporal scales, those of biological organization are relevant for interpreting natural patterns and processes. The organizational scales range hierarchically from subatomic particles to the whole biosphere (e.g. Mayr 1997). The properties of an organizational entity emerge from those of its inferior hierarchical entities and are confined by those of its superior hierarchical entities (Paper III). For instance, the properties of a population emerge from the individuals that constitute it and are confined by the community of which it is a part (Papers III and IV).

Since the hierarchical structure applies to all three types of scales, understanding patterns at one scale generally involves studying processes at another one or vice versa (Paper III). In other words, patterns (or processes) may emerge collectively from large ensembles of smaller scale units or be imposed by larger scale constraints (Levin 1992). For instance, a local community is composed from a regional pool of organisms. The pool, in turn, is shaped by regional patterns such as the geology and climate of the region and long-term ecological and evolutionary processes such as succession and speciation (Huston 1999, Lawton 2000). Since ecological systems vary characteristically on a range of spatial, temporal, and organizational scales, it is crucial to identify the

processes that cause the observed patterns. This can be accomplished only by perceiving the appropriate scales (Witman et al. 2004). Accordingly, to understand how zooplankton composition varies at landscape-level, not only various spatial but also several temporal and organizational scales need to be addressed, as was done in the different papers of this thesis.

1.1.4 Covering variation

Natural patterns such as those of community composition often vary gradually, sometimes more abruptly but seldom in a completely consistent manner. If the extent of variation is not known, it is reasonable to start by addressing the extremes (the ends and/or turning points) in the hypothetical gradient of change (Papers I, II and III). In practice, it is convenient to observe a small number of units or cases that maximize the diversity relevant to the research question (Patton 1990).

The abstraction of compositional patterns into qualitative and quantitative aspects (see also Chapter 1.1.2) is useful for defining the extremes and thus for capturing the relevant variation. Patterns of zooplankton composition are related to quantitative features in their environment by addressing flads representing respective ends of the landscape-level trophic gradient (Paper I) and to qualitative features by addressing flads typifying the three alternative (stable) community states in the region (Papers II and III). This maximum variation approach is also applied to assess how qualitative and quantitative changes in fundamental community components associated with those (trophic and community) states affect processes of zooplankton composition. Various combinations of different foundation, core and keystone species are studied without altering their quantity (Paper III). Conversely, the relative quantities of different community components are manipulated according to different scenarios without changing any of the components (Paper IV). In summary, focusing on qualitative and quantitative extremes is supposed to give a good overview of the direction and extent of variation in the natural patterns of interest and the processes behind them.

1.2 Study system

Although littoral zooplankton had been very little investigated in the northern Baltic prior to this thesis (Paper I) and is a poorly characterized and understood component of brackish and marine systems in general, zooplankton in flads was considered as a good model system for understanding how patterns and processes of community composition can change with the trophic state of the environment. Zooplankton in corresponding freshwater systems has been studied extensively (Lampert 1997), and the abiotic properties of flads make them favorable study environments in many respects.

1.2.1 Zooplankton

Zooplankton plays a pivotal role as a structural and functional mediator in marine (Banse 1995) and freshwater ecosystems (Lampert 1997). These lower order consumers (heterotrophs and detritivores) fuse together the microbial loop and the photosynthetic pathway and thus constitute a major trophic link between a myriad of primary producers and higher order consumers (Pomeroy 1974, Steele 1998). By constituting the principal interface between the cascades of bottom-up and top-down effects (Hairston et al. 1960, McQueen et al. 1986, 1989), zooplankton is intimately involved in a vast range of fundamental ecosystem processes that shape the abiotic and biotic environment. Consequently, zooplankton provides a vantage point to consider community composition.

Zooplankton grazing drives the vertical particle flux in the water column (Kiørboe 1998). This affects the distribution of available nutrients, and thus the composition and distribution of benthic and pelagic organisms. Zooplankton may shape the composition of phytoplankton communities (Haney 1973, Brett et al. 1994, Sommer et al. 2001), limit their total productivity (Brooks and Dodson 1965, Jeppesen et al. 1990, Muylaert et al. 2006) and thus regulate the balance between different ecosystem regimes or community states (Jeppesen et al. 1998, Scheffer 1998, Perrow et al. 1999). Possible shifts between such regimes and states are consequential for the whole ecosystem structure (e.g. Scheffer et al. 1993, Scheffer 1998, Österblom et al. 2007). As a source of food, zooplankton is important for pelagic and benthic invertebrates (Albertson and Leonardson 2001, Viherluoto and Viitasalo 2001) as well as for fish (Mehner and Thiel 1999, Elliott and Hemingway 2002). The availability of suitable zooplankton at the right time and place is particularly crucial for fish-larvae (Cushing 1990). In addition to predation losses, this kind of matching is considered the most important factor controlling the cohort strength in many fish populations (Mehner and Thiel 1999, Harris et al. 2000). Consequently, zooplankton can have long-term effects on the demography of fish populations (Flinkman et al. 1998, Rothschild 1998) and on the composition and productivity of entire fish communities (Werner and Hall 1988, Arrhenius 1996, Hakala et al. 2003).

1.2.2 Flads

The northern Baltic Sea is characterized by its vast mosaic-like archipelagos consisting of thousands of small islands. Due to the planar profile of the region and the extensive length of the aggregate shoreline, the littoral zone constitutes a large proportion of the northern Baltic. Since the Earth's crust is constantly rising in the region along with the so called post-glacial rebound (Lambeck et al. 1998), lagoon-like inlets are abundant in the shores of the northern Baltic. These lagoons, or flads (Ingmar 1975, Munsterhjelm 1997, 2005), are convenient model environments. Firstly, they represent a wide range of environmental conditions at the landscape level (Appelgren and Mattila 2005, Hansen 2010). It is thus easy to cover landscape-level

gradients in, for instance, salinity, degree of isolation or trophic state by using flads as model systems. Secondly, flads are, in marine and brackish contexts, distinctive ecological units with rather clear-cut physical boundaries. In addition to being excellent model environments, the numerous flads of the northern Baltic are regionally important ecological units. Like other shallow inlets in the sea, they function as coastal filters for nutrient run-off and are thus highly important for the biological productivity of the whole region (McGlathery et al. 2007). Consequently, flads are also important targets for conservational measures (Wallström et al. 2000).

Several features, such as topography, the composition of macrophytes and habitat structure, are common for flads and shallow temperate lakes (Scheffer 1998). However, there are also clear differences mainly due to the higher salinity and the connection to the surrounding sea areas which can influence the ecosystem structure and dynamics in the flads.

1.3 General changes in community state associated with the trophic state of the environment

1.3.1 Qualitative changes

Foundation, core and keystone species change along trophic gradients and are thus likely to be intimately involved in the way that the whole community changes. Due to their structural or functional attributes, foundation species create and define entire ecological communities or ecosystems. Although all of the foundation species considered in this study are macrophytes, also sessile animals such as blue mussels (*Mytilus edulis*) can play this kind of role (Westerbom 2006, Koivisto 2011). In contrast, keystone species are usually top predators, whilst core species are basically locally abundant and regionally common (Ellison et al. 2005). The common feature among foundation, keystone and core species is that all can have dramatic effects on their community and thus on ecosystem function and stability (Papers II and III). Common reed (*Phragmites australis*), sago pondweed (*Potamogeton pectinatus*) and coral stonewort (*Chara tomentosa*) are the three most dominant macrophyte species in northern Baltic flads (Snickars et al. 2009, Rosqvist et al. 2010). Thus, they can be regarded as foundation species in those environments. By the same token, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) can be considered as potential core species (Snickars et al. 2009). Especially the abundant young-of-the-year (YOY) of both species can impact zooplankton composition considerably. This impact is likely to depend especially on foundation species and on the trophic structure of the food web (Mehner and Thiel 1999). Further, adult perch are among the top predators in many systems and seem to play an especially important role in flad environments (Järvinen 2005 and references therein). Perch can thus be considered also a keystone species (Paper III).

1.3.2 Quantitative changes

Biological productivity tends to co-vary with the trophic state of the environment (Lindeman 1942). This does not only mean a general increase in the standing stock biomass throughout the food web. Also the trophic structure of communities (i.e. the distribution of biomass among different trophic levels) often changes with the trophic state of the environment (Abrams 1993, Davis et al. 2010). In some cases, the densities of foundation, core and keystone species co-vary with each other and the trophic state of the environment. In other cases, the densities of the different community components change disproportionately. The relative densities of those components are of crucial importance since trophic (and other biological) interactions are density-dependent (Johnson 2006, Hutchinson and Wazer 2007, Ioannou et al. 2008). The ways that the foundation, core and keystone species are involved in composing zooplankton may thus vary with the trophic state of the environment, because not only the identities but also the densities of all interacting organisms co-vary with it (Paper IV).

1.4 Changes in zooplankton composition associated with the trophic state of the environment

Patterns of zooplankton composition tend to change with the trophic state of the environment in temperate lakes (Scheffer 1998, Tallberg et al. 1999, Gyllström et al. 2005) and in the coastal (Johansson 1992, Uitto et al. 1997) and open (Viitasalo 1994, Ojaveer et al. 1998) pelagial of the northern Baltic (Paper I). Systems in low trophic state are generally characterized by K-selected zooplankters such as copepods (Allan 1976). In contrast, systems in high trophic state are often typified by r-selected species such as small-sized herbivorous rotifers and cladocerans (Gannon and Stemberger 1978). Changes in the trophic state of the environment are mediated into zooplankton concurrently by the abiotic environment (Blancher 1984), by competition for food (Makarewicz and Likens 1979, Dumont et al. 1981), by predation from zooplanktivorous fish, insects, larger crustaceans and other zooplankton (Hrbáček et al. 1961, Brooks and Dodson 1965, Brönmark and Hansson 2005) and by higher order predators through trophic cascades (Carpenter et al. 1985). In summary, both bottom-up and top-down processes are important as zooplankton composition changes with the trophic state of the environment (Jeppesen et al. 2000).

1.4.1 Changes in the bottom-up control of zooplankton: food resources and foundation species

In the littoral, the principal food resources of zooplankton are phytoplankton and other planktic microalgae, periphyton, detritus and other zooplankton (Suthers and Rissik 2009). Planktic microalgae and periphyton compete against macrophytes for nutrients (Wium-Andersen et al. 1982, Ozimek et al. 1990, van Donk et al. 1993, Weisner et al. 1994). Furthermore,

the distribution of planktic microalgae, periphyton and the other food resources is partly regulated by the physical structure of the environment, often formed by macrophytes. The different structures can impact small-scale water currents and light conditions and thus the distribution of any seston in the water column (Fonseca and Fisher 1986, Barko and James 1998, Madsen et al. 2001, van de Bund et al. 2004). Seston may also settle on macrophytes and other physical structures. Moreover, periphyton and some small animals use such structures as substrate (Paterson 1993, Lauridsen et al. 1996). Furthermore, movement among structurally varying habitats is important in trophic interactions. For instance, zooplankton and the juvenile fish that prey upon them can migrate between different structures probably as an optimal foraging strategy (Timms and Moss 1984, Persson and Eklöv 1995, Schriver et al. 1995, Burks et al. 2001, Burks et al. 2002). Macrophytes and other structures also affect the distribution of piscivorous fish and the deposition of fish eggs (Lammens 1989, Persson et al. 1993, Schmitz and Suttle 2001, Schultz and Kruschel 2010), which has indirect effects on zooplankton.

As the trophic state of the environment increases, community composition does not change towards any particular direction (Paper II). On the contrary, communities may develop into divergent community states. In aquatic environments, these states are conventionally reflected by primary producers (e.g. McGlathery et al. 2007, Scheffer and van Nes 2007), because they are directly affected by the nutrient availability. Submerged macrophytes, i.e. vascular plants and macroalgae, are often approached by studies focusing on community structure and thus deciphering the vegetative (community) state of the environment (Paper II). In contrast, planktic microalgae and other primary producers are usually viewed as one or a few functional entities (e.g. Jeppesen et al. 1998, van Donk and van de Bund 2002). Yet, changes in microalgal plankton structure along spatial and/or temporal trophic gradients have been characterized in shallow temperate lakes (Duarte et al. 1992, Jensen et al. 1994, Scheffer et al. 1997, Jeppesen et al. 2000).

As primary producers interchange along trophic gradients, gradual replacement of species can sometimes become interrupted by more dramatic shifts into contrasting community states (Scheffer et al. 1993, Scheffer and van Nes 2007). In shallow lakes, the state of the community typically shifts from a submerged plant-dominated one with clear water to a phytoplankton-dominated one with turbid water (Phillips et al. 1978). Submerged macrophytes often give way also to stoneworts (i.e. charophytes) (Hargeby et al. 1994) or floating plants (Scheffer et al. 2003) as the trophic state of the environment increases. All of the different states can also be viewed as alternative stable states (Lewontin 1969, Holling 1973, May 1977). Also in shallow inlets in the sea, primary production shifts from submerged plants towards phytoplankton (Viaroli et al. 2008). This often happens through phases involving opportunistic and usually epiphytic macroalgae (Valiela et al. 1997, Dahlgren and Kautsky 2004). Although less abrupt than in lakes, these transitions are often considered as switches into alternative states (Sand-Jensen and Borum 1991,

Schramm 1999, Orfanidis et al. 2003, Dahlgren and Kautsky 2004, Viaroli et al. 2008).

The relationship between the trophic and vegetative states of flads has been thoroughly characterized (Munsterhjelm 2005, Rosqvist 2010). Flads in the lower end of the natural trophic gradient (Paper II) are typified by diverse (S > 15) macrophyte communities taking up a relatively low share of the flad volume. Common reed and sago pondweed are often the most dominant species. At the opposite end of the trophic gradient, the communities are usually completely dominated by one or two species. Commonly, either a vascular plant (usually pondweed) or a stonewort (usually coral stonewort) dominates the community of submerged macrophytes. In either case, also the emergent reed has a dominant role in the more eutrophic systems (Appelgren and Mattila 2005). Further, macrophyte densities may become very high in those systems. The three depicted community or vegetative states have also been regarded as distinctive regimes (Rosqvist et al. 2010). In addition, local anthropogenic disturbance (eutrophication and dredging) has in many cases led to a phytoplankton-dominated, turbid state (e.g. Rosqvist 2010).

1.4.2 Changes in the top-down control of zooplankton: core planktivores and key piscivores

On top of abiotic conditions, the impact of foundation species on zooplankton composition is likely to depend on the structure of the consumer community. Also fish composition has been strongly attributed to the trophic state of the environment in both freshwater and brackish environments (e.g. Persson et al. 1991, Lappalainen et al. 2001, Olin et al. 2002, Tammi et al. 2003). Lake communities commonly shift from salmonid-dominated ones through percid- and/or esocid-dominated ones to cyprinid-dominated ones (Svärdson 1976, Hartmann and Nümann 1977, Leach et al. 1977, Persson 1983, Kubecka 1993). Importantly, the latter shift is also associated with a transition from piscivore- to planktivore-dominated communities (Persson 1986, Persson and Greenberg 1990, Jeppesen et al. 2000). These kinds of changes in the trophic structure of the food web are highly consequential for the structure and function of zooplankton communities (Leibold 1990, Hansson 1992, Persson et al. 1992, Wurtsbaugh 1992, Flecker and Townsend 1994, Mazumder 1994, McIntosh and Townsend 1994, Brett and Goldman 1997).

Also in the Baltic Sea, coastal fish communities shift from percid to cyprinid domination as the trophic state of the environment increases (Anttila 1973, Hansson 1987, Lappalainen et al. 2000). Corresponding patterns have been found in flads (Järvinen 2005, Snickars et al. 2009). Of the core planktivores in littoral environments, YOY perch prefer densely vegetated habitats, especially in the presence of potential predators (Snickars et al. 2004, 2009). In contrast, YOY roach prefer more open habitats of the littoral at low predation risk, and exhibit two differing anti-predator strategies when the risk is elevated. They either seek refuge in vegetation or aggregate in shoals in the open habitats (Huckstorf et al. 2009). YOY perch are generally

considered better at foraging in dense vegetation than YOY roach, whereas roach are thought to have the advantage in open habitats (Diehl 1988). Perch and roach have a complex competitive and trophic relationship. As juveniles, the species compete for zooplankton. If perch are able to reach a sufficient size (in spite of intra- and interspecific competition), they may start preying upon smaller perch and roach (Eklöv and Persson 1995, Persson and Eklöv 1995). These different scenarios are highly consequential for zooplankton composition and *vice versa*.

1.5 Habitat complexity as a link between bottom-up and top-down control

Habitat complexity is one of the most central concepts in this thesis, because it links together bottom-up and top-down processes of community composition. Habitat complexity does not necessarily constitute a trophic component in those processes, and it can rather be considered as more of a moderating element. The impact that foundation species have on their environment may thus not be fully appreciated if (in addition to being trophic components in a system) they are not viewed through the concept of habitat complexity (Paper III).

Habitat complexity often arises from macrophytes, varies with their identity and density and thus defines structural habitats with given complexity (Bell et al. 1991). Habitat complexity plays a versatile role in structuring communities by being involved in various endogenous processes. It can impact resource acquisition (Karr 1976, Minshall 1984), competition (Werner and Hall 1979, Sih et al. 1985) and predator-prey interactions (Bowman and Harris 1980, Verdolin 2006) and may thus greatly contribute to community composition. Importantly, these processes also impact each other (e.g. Vandermeer 1972), because they take place among the members of the community and are manifested as its composition (Odum 1977). Consequently, a community responds to habitat complexity as an entity, each constituent organism in its own individual but community-dependent way. Moreover, abiotic conditions alter the role of habitat complexity through exogenous processes. First, exogenous processes determine the pool of members of which a local community is composed (Gaston et al. 2003, Mora et al. 2003), also those that constitute habitat complexity (e.g. Barko et al. 1986, Lavorel and Garnier 2002). Thus, exogenous processes indirectly define the network of endogenous processes, including those involving habitat complexity, within the community. Secondly, exogenous processes may also alter the impact of habitat complexity on the endogenous processes structuring communities within a given assemblage. Processes such as wave action have a direct impact on habitat complexity (Smokorowski and Pratt 2007), whereas other processes such as increase in water turbidity can impact the way habitat complexity modifies endogenous processes such as predator-prey interactions (Snickars et al. 2004, Pekcan-Hekim et al. 2010).

2 Methods

2.1 Surveying change in patterns of zooplankton composition in relation to the trophic state of the flads

The structure and seasonal dynamics of zooplankton were surveyed in relation to environmental conditions (salinity, temperature, turbidity, oxygen content, and concentrations of total phosphorus, total nitrogen and chlorophyll *a*) in four flads (Figure 1) (Paper I). They where chosen from 20 tentatively surveyed lagoons in the Åland Islands (Snickars et al. 2009) and were supposed to typify respective ends of the landscape-level gradient in trophic state. Although the three principal community states (see Chapter 1.4.1) that have been described for northern Baltic lagoons (Rosqvist et al. 2010) were represented in the studied flads (Paper II), Paper I was not designed to take this aspect into consideration. Hamnflada (MHF) and Norrflada (MNF) represented flads in comparably low and Mjärdvik (EMV) and Notgrund (ENG) in comparably high trophic states.

2.2 Surveying change in community state in relation to the trophic state of the flads

The study flads (Paper I) were revisited during another growth season to examine seasonal variation in microalgal plankton composition in relation to abiotic conditions, macrophytes (Paper II) and zooplankton (Paper III). Since the flads appear to represent the three alternative stable states in the region (Rosqvist 2010), they should cover the regional gamut of microalgal plankton as extensively as possible. The species composition and horizontal and vertical coverage of macrophytes, their epiphytes and drifting algae were registered in the field. Microalgal plankton was sampled in two contiguous habitats with contrasting complexity to take into account the local, structuring role of foundation species. One of the habitats consisted of, for each flad, maximally dense monoculture of the most important foundation species (see chapter 1.4.1). The other habitat was an equally large (ca 2 m^2) area with bare bottom (Papers II and III). The plankton samples were taken at midday and at midnight to take into account diurnal variation.
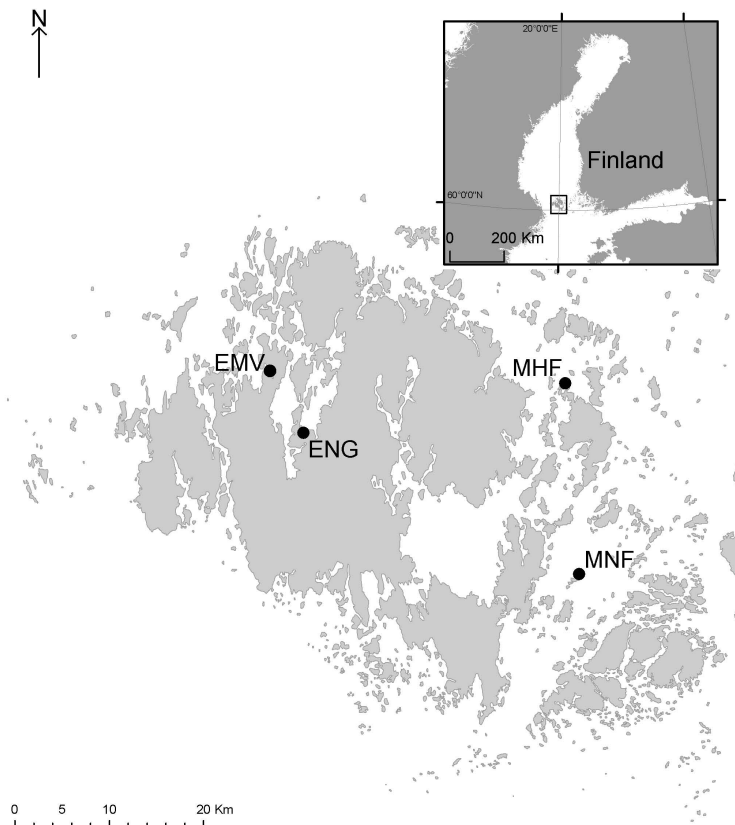
Figure 1. The surveyed flads are located in the archipelago of the Åland Islands. Hamnflada (MHF) and Norrflada (MNF) represent flads in comparably low and Mjärdvik (EMV) and Notgrund (ENG) in comparably high trophic state.

2.3 Assessing zooplankton composition in relation to community state

2.3.1 Qualitative aspects

Patterns and processes of littoral zooplankton composition were compared among communities representing alternative community states. The focus was placed on the local structuring role of habitat complexity by comparing the composition of natural zooplankton associations between two contiguous habitats with contrasting complexity (Paper III). Zooplankton was sampled in the field together with microalgal plankton (see Chapter 2.2). The same sampling set-up was also utilized in mesocosms. The principal aims were to clarify how the structuring role of habitat complexity in community composition (defined as the difference or similarity of zooplankton between the two contiguous habitats with contrasting complexity) varies among the members of a natural zooplankton association and how the structuring role varies, as the members of the community change together with their environment.

The structuring role of habitat complexity was studied first in mesocosms. The composition of foundation species (common reed and sago pondweed), core zooplanktivores (YOY perch and YOY roach) and keystone piscivores (adult perch) was manipulated simulating possible scenarios of change in community state, associated with variation in the trophic state of the study flads. The individual and concurrent impacts of these community components were assessed at different times of the day to take into account a generally important exogenous factor. The generality and practical relevance of the experimental findings were then evaluated in the field. The sampling set-up of the mesocosm study was applied in a whole-growth-season field survey in the four study flads representing contrasting trophic and alternative community states (cp. Chapter 2.2).

2.3.2 Quantitative aspects

Several series of manipulative mesocosm experiments were implemented to assess how different changes in organism densities can affect zooplanktivory. Two different scenarios of change in community state were compared with each other. In the first scenario, the densities of foundation species (and thus habitat complexity) increase, whilst those of zooplankton and core zooplanktivores remain constant (Figure 2a). In the second scenario, the densities of all three components increase together (Figure 2b). In order to assess the impact of foundation species on zooplanktivory in the two scenarios, two principal series of experiments – the *fixed density* and the *dynamic density series* – and two ancillary ones were carried out. In the fixed density series, constant densities of zooplankton and zooplanktivores were exposed to four levels of foundation species densities. In the dynamic density series, the densities of zooplankton and zooplanktivores co-varied with those foundation species densities.

The ancillary series (Figures 2c and 2d) were needed to explain the outcome of the dynamic density scenario. On one hand, an increase in vegetation density is known to decrease encounters between predators and prey (Murdoch and Oaten 1975, Manatunge et al. 2000, Turesson and Brönmark 2007). On the other hand, these kinds of encounters increase with increasing animal densities (Johnson 2006, Hutchinson and Wazer 2007, Ioannou et al. 2008). These two mechanisms, the vegetation-density-based and the animal-density-based, should thus counteract each other in conditions where the densities of foundation species and associated animals, including both zooplankton and zooplanktivores, co-vary. The ancillary series were used to segregate and quantify those mechanisms and thus to evaluate the paradigm of attributing high densities of lower order consumers in densely vegetated habitats to the protective value of foundation species (i.e. to decreased numbers of encounters with predators). All the experiments were run with two alternative core zooplanktivores, YOY perch and YOY roach. Structures resembling sago pondweed were used to mimic foundation species. *Daphnia* (*Daphnia magna*) were used as prey.

3 Results and discussion

3.1 Littoral zooplankton changes with the trophic state of the environment

Zooplankton abundance and diversity were assessed in relation to the productivity potential of the environment to encapsulate much of the landscape-level variation associated with littoral zooplankton and to link the patterns to ecosystem functioning (e.g. Johansson 1992, Attayde and Bozelli 1998, Jeppesen et al. 2000, Barnett and Beisner 2007) (Paper I).

Zooplankton abundance correlated positively with the trophic state of the environment, similarly to the situation in temperate lakes (Scheffer 1998, Tallberg et al. 1999, Gyllström et al. 2005) and in the coastal (Johansson 1992, Uitto et al. 1997) and open (Viitasalo 1994, Ojaveer et al. 1998) pelagial of the northern Baltic. As in shallow temperate lakes (Scheffer 1998, Jeppesen et al. 2000) and in contrast to the situation in northern Baltic pelagial (Johansson 1992, Viitasalo 1994, Viitasalo et al. 1995, Uitto et al. 1997), seasonal succession was early, the earlier the higher the trophic state of the environment. The variation among the flads can be attributed to differences in water temperature and in the flow of detritus and nutrients from land especially early on in the spring (e.g. Sobczak et al. 2005).

Although zooplankton α-diversity is often unimodally related to the trophic state of the environment (Barnett and Beisner 2007), variation among the study flads was negligible. Productivity and the magnitude of other ecosystem functions such as nutrient cycling and decomposition (Hooper et al. 2005) are believed to vary with α-diversity mainly due to complementarity (different species partitioning resources) and to some extent also to selection effects (the higher chance of a really productive species being included in a community with many species) (Balvanera et al. 2006). Even if zooplankton production was examined only through snapshots (standing stock biomass), no particular relationship seemed to exist between zooplankton productivity and α-diversity. Distinguishing between patterns associated with complementarity and selection could be interesting in such a scenario. Instead of these correlative patterns (selection and complementarity are not mechanisms), there are processes that can generally explain landscape-level variation in the density and diversity of zooplankton. These processes are commonly attributed to the diversity of food resources, spatio-temporal heterogeneity in food abundance, habitat variability and predation intensity (Hutchinson 1961, Brooks and Dodson 1965, Waide et al. 1999, Mittelbach et al. 2001). Investigating these processes was thus deemed as crucial for understanding the observed patterns.

Finally, zooplankton β-diversity seemed clearly associated with the trophic state of the environment. In other words, zooplankton composition differed distinctively among flads representing different trophic states. Compositional variation among the flads generally decreased over the season (Paper I), and the difference between mesotrophic and eutrophic flads became less clear by late summer. Importantly, the change along the trophic gradient seemed to be inconsistent. In spite of the clear division into mesotrophic and eutrophic zooplankton community types, differences between the eutrophic flads were still considerable. They seemed to be represented by two yet distinctive community types.

3.2 Planktic microalgae and macrophytes reflect how community state changes with trophic state

The three (vegetative) community states (see 1.4.1) that the study flads were expected to represent proved to be distinctive throughout the season (Figure 3 in Paper II). Microalgal plankton associations varied primarily at large spatial and temporal scales, i.e. among the flads and over the season. The compositional variation was more distinctively associated with the vegetative than with the trophic state of the flads (Figure 6 in Paper II). However, the functional properties of the studied microalgal plankton associations, such as their total abundance and α-diversity, were generally more clearly related to the trophic than to the vegetative state of the flads (Figure 7 in Paper II). In both cases, variation in microalgal plankton structure was generally greatest during early and mid-season, from May until August. During the late season, in September and October, microalgal plankton became comparably uniform in all flads. Local and diurnal variation in microalgal plankton composition was inconsistent and weak. In other words, this small-scale variation depended on the landscape-level and seasonal patterns and was comparatively much smaller. The most prominent differences in microalgal plankton composition between open water and adjacent dense monocultures of foundation species were present in the eutrophic flads, especially in the stonewort-dominated ENG, during early season, in May and June (Figures 6 and 7 in Paper II).

Substantial changes in patterns of microalgal plankton composition associated with the trophic state of the environment have also been reported in several studies conducted in shallow lakes (Kalff and Knoechl 1978, Duarte et al. 1992, Jensen et al. 1994, Pedersen and Borum 1996, Watson et al. 1997, Scheffer et al. 1997, Jeppesen et al. 2000). Changes in the relative quantity of main microalgal plankton divisions over the studied trophic gradient correspond mainly to those described for similar gradients in shallow lakes (Figure 5 in Paper II). However, this does not apply to ENG, although patterns within the flad (seasonal, local and diurnal variation) were consistent with observations in shallow lakes (Balls et al. 1989, van Donk et al. 1990).

Microalgal plankton composition can vary with that of macrophytes because (1) both types of primary producers are shaped by certain common factors such as the trophic state of the environment and/or (2) the primary producers regulate each others' composition. In general, macrophytes and planktic microalgae affect each other in many ways by competing for and modifying the availability of light and nutrients (Barko and James 1998, Mulderij et al. 2007). Additionally, macrophytes can increase the sinking loss of phytoplankters (van de Bund et al. 2004) and produce allelopathic compounds against these organisms (Wium-Andersen et al. 1982). However, sago

pondweed is not known to produce allelopathic substances (Körner and Nicklisch 2002), and the allelopathic potential of Charophytes is thought to be low (Mulderij et al. 2007). There can also be indirect influences between planktic microalgae and macrophytes. Both planktic microalgae and macrophytes can modify trophic interactions at several trophic levels, physically and chemically (Timms and Moss 1984, Persson and Eklöv 1995, Lauridsen and Lodge 1996, Burks et al. 2000). These kinds of effects on different consumer levels can cascade down to either group of primary producers (Carpenter et al. 1985, Scheffer et al. 1993).

The magnitude of landscape-level variation in microalgal plankton composition may correlate with the local, structuring importance of macrophytes. Accordingly, this importance may be smallest in the mesotrophic flads and largest in the stonewort-dominated, eutrophic one. However, this applies only to the local-level processes in which macrophytes are involved. That is, different processes may be responsible for shaping microalgal plankton communities at local and landscape levels. The structuring role of macrophytes can thus be important also in the mesotrophic flads even though microalgal plankton composition did not differ between macrophytes and open water in those flads.

Local and diurnal variation in microalgal plankton composition should be highly important for zooplankton. The availability of planktic microalgae should, together with the availability of other food resources (such as bacteria and detritus), competition and predation, determine the distribution of zooplankton among habitats differing in complexity and thus the local composition of zooplankton.

3.3 Processes of zooplankton composition change with community state – qualitative aspects

Manipulative experiments in mesocosms and mensurative surveys in the field demonstrated that qualitative (abiotic and biotic) changes associated with variation in trophic and community states are reflected in processes of zooplankton composition (Paper III). Habitat complexity formed by macrophytes played a central role in these processes. The manipulative experiments showed that this role varied depending on the zooplankton group, and further, depending on qualitative changes in community composition and in the abiotic environment. The field studies confirmed that patterns of zooplankton composition were strongly associated with the vegetative state of the environment, both at the local and the landscape level.

Active migration and predation mortality determined the local distribution of zooplankton in the mesocosm experiments (Figure 1 in Paper III). Similar environmental conditions were reflected differently by different functional groups (Figures 1 and 2 in Paper III). Some groups were concentrated in the open water, others in the foundation species, whilst still others were evenly distributed between those habitat types. The distribution patterns correlated with the traits used for the functional classification (Odum and Heald 1975, Christian and Luczkovich 1999). The tendency to get

concentrated into either habitat type was associated with body size and expected mobility. In practice, large crustaceans, cladocerans and copepods were often accumulated either in open water or in macrophytes. In contrast, smaller organisms, the different rotifer groups and the copepod nauplii, were often evenly distributed between the different habitats. Furthermore, the functional groups differed from each other in their responses to changes in environmental conditions. Different macrophyte species affected local zooplankton composition depending on the identity of planktivores, on the trophic structure of the experimental food web (presence/absence of keystone piscivore) and on the time of day. In some cases, these other factors played important roles in determining the composition of zooplankton even regardless of macrophyte species.

Zooplankton composition varied distinctively among and within the flads, i.e. at landscape and local scales as well as over the season and between different times of the day, i.e. at seasonal and diurnal scales (Figure 3 in Paper III). Local variation was generally smallest in the flads in low trophic state (MHF and MNF), larger in the pondweed-dominated eutrophic flad (EMV) and largest in the stonewort-dominated eutrophic flad (ENG). Variation among the flads was associated with both the trophic and the vegetative states of the environment. The extent of this landscape-level variation depended on both local and diurnal variation. Zooplankton was relatively similar in both mesotrophic flads and differed clearly from that in the eutrophic flads regardless of the habitat type and the time of the day. In contrast, there were large differences between the eutrophic flads. The pondweed-dominated flad differed less and the stonewort-dominated flad more from the mesotrophic flads in their zooplankton composition. This pattern was stronger for the zooplankton residing in the dominant macrophyte species than for that in the open water, especially during daytime.

3.3.1 The structuring role of habitat complexity varies among zooplankton

Distributional variation among the functional groups can be explained by three types of phenomena. Firstly, if factors controlling turnover (natality and mortality) differ between habitats with different complexity, then the way that functional groups are distributed between them should also vary (Vince et al. 1976, Jeffries and Lawton 1984). These factors tend to vary depending on the group. Secondly, the same factors, or rather changes in them, may also trigger migrations between habitats with differing complexity (Timms and Moss 1984, Burks et al. 2000, Johnson 2006). Such migrations can also be passive. Periodical or random changes in the abiotic environment may induce water currents from one type of structural habitat to another, causing members of particular functional groups to switch habitat type (Walters and Bell 1986, Suh and Yu 1996). Thirdly, the concurrent impact of turnover and migrations can also vary among the constituents of a functional group (Lassau et al. 2005). An even distribution between the habitat types may thus actually reflect only an accumulation of some constituents

(species, size-classes, ontogenetic stages etc.) in open water and of others in macrophytes. This is not at all unlikely, since the members of a functional group have, by definition, considerably overlapping niches (Blaum et al. 2011). In order for competition to be minimal within such a group, some of its members should therefore become dispersed in space and time and thus not necessarily occupy the same habitats at the same time (e.g. Vandermeer 1972). This kind of dispersal can be passive or active (Kaitala et al. 1993, Chapman et al. 2011).

3.3.2 The structuring role of habitat complexity depends on how patterns of community composition change with the trophic state of the environment

Macrophyte identity proved to be a central factor in determining local-level zooplankton distribution (Figure 3 in Paper 3). In other words, the structuring role of habitat complexity varied strongly with the architecture of the foundation species. Although several field experiments on artificial macrophytes with varying architecture (e.g. Schriver et al. 1995, Meerhoff et al. 2007) have stressed the importance of foundation species identity in influencing zooplankton composition, they have provided no causal evidence on how the effects of foundation species depend on other environmental factors.

The way the local distribution of zooplankton was affected by macrophyte identity depended on the time of the day (Figure 1 in Paper 3). Such diurnal changes in zooplankton composition among stands of certain macrophyte species and open water areas are relatively well documented in shallow lakes. By night, some zooplankton may perform diel horizontal migrations (DHM) from macrophytes into open water (Timms and Moss 1984) or from open water to macrophytes (Nurminen and Horppila 2002, Meerhoff et al. 2007), i.e. reversed horizontal migrations (RHM). By day, the directions are reversed. Such active horizontal and corresponding diel vertical migrations (DVM) (Forel 1878, Hays 2003) are thought to be a form of anti-predator behavior where the distribution of some organizational unit of zooplankton (a species, a functional group or even the whole community) becomes concentrated in one type of habitat by night and in another type by day. In contrast, local zooplankton distribution in the mesocosms varied rather between hetero- and homogeneous states. Where and when zooplankton was accumulated depended on the identity of foundation species and the time of the day, and as stated earlier, on the zooplankter.

The diurnal alternation between locally hetero- and homogeneous distributions conforms to predictions based on optimal foraging models (e.g. Abrams 1982). Firstly, the foraging behavior and habitat choice of both experimental zooplanktivores are known to depend extensively on the time of day (Diehl 1988, Persson and Eklöv 1995). Accordingly, perch utilized the whole mesocosm at night and became concentrated in the macrophytes by day, whilst roach exhibited opposite diurnal patterning. Secondly, planktic primary producers, the basic food resource for zooplankton, were evenly distributed between the habitat types regardless of any environmental conditions, thus reflecting patterns in the field (Paper II). In other words, food availability did not differ between the habitats with contrasting complexity, whereas the corresponding difference in predation pressure varied diurnally. For zooplankton, the concurrent impacts of predation pressure and resource availability should thus cause active (migration) and/or passive (mortality) diurnal alternation between hetero- and homogeneous states rather than accumulation in one habitat type at one time of the day and in another at a different time of the day. The latter scenario would occur if also resource availability and not simply predation pressure differed between two alternative habitats, like phytoplankton availability does in DVM (Hays 2003).

The way the local distribution of zooplankton was affected by macrophyte identity depended also on the number of trophic levels in the experimental food web (Figure 1 in Paper III). This was manifested especially in the trophic structure of zooplankton. The experimental findings thus support the idea that the mere presence of higher order consumers can fundamentally influence the way that foundation species structure associations of lower order consumers (Diehl 1988, Grabowski 2004, Griffen 2006, Griffen and Williamson 2008, Martin et al. 2010).

Planktivore identity had fundamental impacts on the local distribution of zooplankton regardless of the identity of foundation species (Figure 1 in Paper III) or any other factor. The impacts were manifested in the size structure of the entire zooplankton community. Zooplankton was generally larger and planktivore densities lower in open water than in the foundation species. As zooplankton body size is known to correlate well with susceptibility to zooplanktivorous fish (e.g. Brooks and Dodson 1965), large-bodied zooplankters may have avoided predation by accumulating (actively or passively) into open water. Large-bodied predatory zooplankton can further have had a cumulative impact on the size structure of the community by preying upon the small-bodied forms. Simultaneously or alternatively, small-bodied zooplankters may have avoided predation by zooplanktivorous fish and plankton by accumulating into vegetation (Nicolle et al. 2010). However, it is likely that perch and roach evoked a polarization in zooplankton size structure through different mechanisms. Accordingly, the difference caused by roach was twice as great as that attributable to perch, although perch was generally the more efficient of the planktivore species (Paper III). This suggests that large zooplankters may have escaped roach by migrating into open water. By contrast, perch can have caused a corresponding (but weaker) accumulation by consuming the large zooplankters in the habitats with foundation species. Although the presence of only one zooplanktivore species does not reflect the natural settings of the studied zooplankton community, the results indicate that zooplanktivore composition may be fundamentally important for the way that habitat complexity structures zooplankton communities.

3.3.3 The structuring role of habitat complexity varies among zooplankton associations and within functional groups representing communities in alternative states

The generally low local variation in zooplankton composition at both ends of the season (Figure 3 in Paper III) coincided with periods generally characterized by comparably low macrophyte volume and low planktivore abundance (Appelgren and Mattila 2005, Snickars et al. 2009, Rosqvist et al. 2010). In contrast, local variation in microalgal plankton composition was noticeable only at the beginning of the season and then only in the eutrophic flads (Figures 6 and 7 in Paper II). The environmental conditions point to two alternative or synergetic explanations for situations where the local variation in zooplankton composition was low. Firstly, zooplankton should not have experienced any direct selection pressure towards either habitat type, as the differences in microalgal plankton availability seemed to be small (Paper II) and predation pressure generally low (Snickars et al. 2009). Secondly, the seasonal succession of zooplankton is likely to co-vary with that of macrophytes. Accordingly, zooplankton with a general tendency to accumulate in macrophytes, particularly herbivorous cladocerans and omni/carnivorous copepods, occurred at low abundances during periods of poor macrophyte cover. This would mean that the co-variation between the composition of macrophytes and zooplankton was manifested as landscape-level rather than as local variation. Reduced abundance of structurally complex habitats can lead to changes in community composition over a wider system consisting of structurally different habitats (Thrush et al. 2001).

Although the overall composition of local zooplankton assemblages and the direct habitat selection pressures varied also within the time frame between May and October, the conditions stayed favorable for inducing local variation in zooplankton composition. Its nature and magnitude varied on the landscape and diurnal scales due to two principal reasons. Firstly, local zooplankton associations, and secondly, the local conditions they are shaped by, vary due to exogenous factors. In other words, the way natural associations of organisms function cannot be separated from the conditions they have been formed by (Schröder and Seppelt 2006).

Regardless of the exact mechanisms, the field results suggest that the trophic state of the environment, foundation species identity and light conditions strongly influence the structuring role of habitat complexity in community composition. In other words, the architecture and other functional properties of foundations species can disrupt the way in which local species assemblages are related to the trophic state of the environment (Brauns et al. 2007).

3.4 Processes of zooplankton composition change with community state – quantitative aspects

The comparison between the two eutrophication-associated scenarios of change in community state confirmed that processes of zooplankton composition not only depend on the identity but also on the density of community components (Paper IV).

In the fixed density scenario, the densities of foundation species increased, while those of zooplankton and core zooplanktivores remained constant (Figure 2a). The increasing density of foundation species caused a decline in the mean predation efficiency of perch while that of roach remained unaffected.

In the dynamic density scenario, the densities of foundation species, zooplankton and the core zooplanktivores increased together (Figure 2b). Mean predation efficiency of both zooplanktivore species increased with the increasing densities of foundation species, although the increase for roach was more or less negligible (and statistically non-significant).

In the vegetation impact series, the set-up of the dynamic density series was repeated without the foundation species (Figure 2c). Regardless of predator species, the patterns of predation efficiency were almost exactly the same as in the dynamic density series. Thus, foundation species had no impact on predation efficiency in that scenario. Accordingly, the patterns in the dynamic density scenario were determined exclusively by the densities of zooplankton and/or the zooplanktivores.

In the predator impact series, the set-up of the dynamic density series was repeated with a 50/50 combination of both planktivore species (Figure 2d). The pattern of predation efficiency was almost exactly the average of the respective (one with perch and the other with roach) dynamic density series. Thus, the shoal size of neither predator species impacted predation efficiency in that scenario. Further, the foraging of neither predator species seemed to be affected by the presence of the other. Thus, the patterns in the dynamic density scenario were determined exclusively by the aggregate animal density.

In summary, the relative density of foundation species, zooplankton and zooplanktivores as well as the traits of the zooplanktivores affected the outcome of interactions among the three components. Depending on zooplanktivore traits, the impact of foundation species on zooplanktivory differed completely between the different change scenarios in community state. Increasing animal densities appeared to be able to cancel out and even override the negative impact of foundation species on zooplanktivory.

According to several studies conducted in aquatic (e.g. Estes and Palmisano 1974, Werner et al. 1983, Summerson and Peterson 1984, Sih et al. 1985, Wootton 1993, Schriver et al. 1995) and terrestrial (e.g. Bowman and Harris 1980, Bell et al. 1991, Verdolin 2006) environments, the density of foundation species and their protective value against predation correlate positively. Indeed, increasing density of foundation species decreases encounters between predators and prey (Murdoch and Oaten 1975, Manatunge et al. 2000, Turesson and Brönmark 2007). Thus, high zooplankton abundance may well be attributable to the protective value of foundation species in conditions where zooplanktivore abundance does not co-vary with foundation species density. Consequently, the protective impact of foundation species can vary

depending on the trophic level of the prey and on the total number of trophic levels in the food-web (e.g. Winfield 1986, Eriksson et al. 2009). For instance, the impact of foundation species on the survival of prey and on its predator can be opposite in the presence of a higher-order predator (e.g. Eklöv and Persson 1995, Persson and Eklöv 1995). Furthermore, prey may also choose to share their habitat with their predator if resource availability (Karr 1976) and competitive pressure (Werner and Hall 1979, Mittelbach 1981) compensate for the increased predation risk (Schoener 1971, Werner and Hall 1988, Walters and Juanes 1993, Walters and Martell 2004).

There are a considerable number of mechanisms other than those directly impacting the probability of encounters between zooplankton and zooplanktivores which may also contribute to the positive correlation between the densities of foundation species and the associated animals. First, the positive correlation can be a result of simple co-variation with the productivity of the environment (e.g. Carr et al. 1997, Polis 1999).

Secondly, foundation species may impact the amount of habitable physical space, perhaps providing new niches for species to exploit (Bell 1985, Bartholomew et al. 2000). Thirdly, predation efficiency can, instead of decreasing, increase with foundation species density. Consequently, the densities of various predators may correlate positively with those of foundation species and prey (Schmitz and Suttle 2001, Horinouchi et al. 2009, Schultz and Kruschel 2010). Finally, the density of foundation species can be strongly shaped by consumers, either directly or indirectly (e.g. Jacobsen et al. 1997, Perrow et al. 1999, Eriksson et al. 2009). In other words, the scenario where the densities of foundation species co-vary with those of associated animals can also be regulated by the animal densities.

In conclusion, competition and resource availability, and not simply predator-prey interactions, need to be considered in order to explain patterns of co-variation among the densities of foundation species, prey and predators.
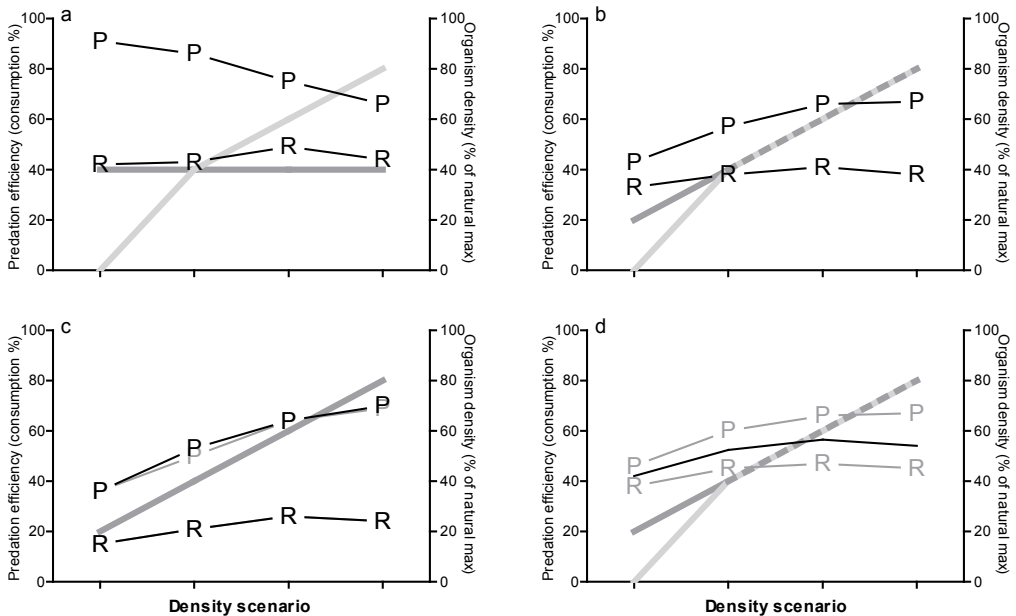
Figure 2a-d. Paper 4 (a). Mean zooplanktivory efficiency (% of *Daphnia* eaten) by YOY perch ((*Perca fluviatilis*) [P]) and by YOY roach ((*Rutilus rutilus*) [R]) at different plant (i.e. foundation species [thick, light grey line]) and animal (i.e. prey and predator [thick, dark grey line]) densities. (a) and (b) represent two different scenarios of change in community state. In (a), the fixed density series (n = 6), plant densities increased whilst those of the associated animals stayed constant. In (b), the dynamic density series (n = 25), animal densities increased in conjunction with those plant densities. In (c), the vegetation impact series (n = 7), the set-up of the dynamic density series was repeated without the plants. The results of the corresponding dynamic density series (only those run in the same blocks) are shown in light grey. In (d), the predator impact series (n = 17), the set-up of the dynamic density series was repeated with a 50/50 combination of both planktivore species instead of using only single species as in all the other series. The results of the corresponding dynamic density series are shown in light grey (like in (c)).

4 Conclusions and future perspectives

4.1 Principal observations

Patterns of zoo- and microalgal plankton composition varied distinctively with the trophic and community states of the flads. This landscape-level variation decreased towards the end of the growth season, in conjunction with variation in the trophic state and in contrast to variation in the vegetative (community) state of the flads. The magnitude of local and diurnal differences in zoo- and microalgal plankton composition increased with the trophic and varied with the community state of the flads and was generally small in both ends of the growth season. Furthermore, the composition of zooplankton varied locally and diurnally considerably more than that of microalgal plankton, suggesting that habitat complexity formed by foundation species is not associated with zooplankton composition through microalgal plankton.

In addition to the quantitative and qualitative co-variation in patterns of foundation species and zooplankton composition at multiple spatial and temporal scales, the manipulative experiments demonstrated that the relative density and diversity of foundation species are intimately involved in processes of zooplankton composition. First, the structuring role of habitat complexity varied among zooplankton groups. Second, the structuring role of habitat complexity varied depending on qualitative community changes associated with the trophic state of the environment. Third, these impacts varied depending on the environmental context such as the time of day. In addition to their assemblage, the relative densities of foundation species, zooplankton and core zooplanktivores exerted fundamental impacts on the structuring role of habitat complexity in zooplanktivory, a central process of zooplankton composition. In a community state scenario where the densities of foundation species increased, while those of zooplankton and core zooplanktivores remained constant, zooplanktivory decreased with increasing habitat complexity. In contrast, this protective relationship did not exist in a scenario where the densities of the three components increased in tandem. Instead, zooplanktivory was determined explicitly by the aggregate density of zooplankton and zooplanktivores. In summary, the impacts that foundation species have on the ambient animal community differ in their type and magnitude depending primarily on the identity and density of the foundation species, secondarily on the trophic position of the interacting animal and the trophic structure of the food web and finally on abiotic environmental conditions.

It has not escaped my notice that factors controlling the identity, traits and density of foundation species (in this study, especially common reed and coral stonewort) point to possibly central mechanisms for regulating the state of the ambient communities. These mechanisms should involve both bottom-up and top-down processes, linked by competition and other types of nontrophic interplay. Although the local role of microalgal plankton as a factor controlling zooplankton composition appears to be smaller than expected, other sources of food such as detritus and bacteria can be relatively more important (e.g. Vadeboncoeur et al. 2002, Bode et al. 2006). Thus, it is important to understand how foundation species affect the distribution of those resources. It is, of course, possible that the bottom-up regulation of zooplankton is generally insignificant compared with its top-down regulation (e.g. Nicolle et al. 2011). Future investigations in the study environments should thus quantify the relative role of different energy pathways leading to zooplankton and relate them further to the corresponding pathways away from zooplankton to higher order consumers. Pathways through other lower order consumers, such as zoobenthos, should also be quantitatively coupled into the prospective food web model. Finally, it should be noted that the structuring role of foundation species is by no means related simply to their physical structure. The way foundation species are related to their abiotic environment, other primary producers and consumers involves a myriad of interconnected mechanisms such as nutrient cycling, allelopathy and herbivory.

Generally speaking, the identification of central ecosystem components, the investigation of how they impact the ambient system and how it affects them should be of primary importance in the disciplines of community and systems ecology. For instance, the trophic state of the environment not only generates patterns of community composition but also is dependent upon those patterns. Instead of studying patterns of biodiversity (species richness, α-diversity, complementarity, selection effects, etc.), the focus should thus be switched to the ecosystem processes and the main ecosystem components that drive these processes (Woodwell 2010). Although these basic ecological concepts and causalities appear self-evident in a theoretical context, they are often ignored. Even if theory clearly emphasizes the inherent context-dependency of ecological (and any biological) phenomena, research programs are always based on given ecological conformities of interest. Consequently, the conformities often turn out confounded or simply lack natural relevance. In other words, the observed patterns do not conform to the theoretical predictions because they are disturbed by unacknowledged circumstances. Alternatively, the theoretical predictions may be accurate but confined to describing correlations among natural patterns. Therefore, the key to prediction and causal understanding of ecological patterns lies in the elucidation of the underlying processes (Levin 1992). A thorough understanding of natural systems thus requires focus on multiple conformities, multiple theoretical frameworks, multiple (spatial, temporal and organizational) scales, and consequently, on multiple systems.

4.2 Theoretical perspectives

The development of the many theoretical frameworks upon which the individual papers are built has been discussed principally in those contexts. Although theoretical development has been the principal aim of this thesis work, the attempt to understand the study system from a broader perspective not only guided the progress of this work but also evolved into an end in

itself. In the individual papers in the thesis, observations and theory matched well in some respects but poorly in others. Observations from the system consolidated some frameworks, changed others and definitely required several frameworks to be explained (Herek 1995). Apart from reducing the concept of productivity to the trophic state of the environment (which was done for practical, not theoretical reasons), the trend has been towards and overarching perspective on the study system that incorporates several theoretical frameworks. So far, unifying concepts seem to be found within classical community ecology. Concepts such as trophic structure and trophic dynamics (Lindeman 1942, Hutchinson 1948), the trophic cascade (Zaret and Paine 1973, Carpenter et al. 1985), and the impacts of competition and predation on community structure (Hutchinson 1961, Hrbáček 1961, Brooks and Dodson 1965) have all been essential for helping to understand the study system. As opposed to e.g. the concept of α-diversity, habitat complexity is not, as such, incorporated in any of the classical concepts. Further, the concept of habitat complexity is focused on the way habitat complexity alters ecological processes, whilst many of the classical concepts are concerned with those very processes. Consequently, the concept of habitat complexity is likely to confer added explanatory value to the other classical frameworks.

Not entirely by chance, the most important theoretical concepts this work has arrived at stem from research in small lakes (Hairston 2005), environments that appear to resemble flads in many respects. One reason for this is that these kinds of lakes can be considered as microcosms (Forbes 1887) for understanding ecological phenomena on a variety of scales. Hopefully, the corresponding properties of flad environments will make also them into prolific natural laboratories. A good approach could be to broaden the perspective on this study system even more and try to fit in all of the classical concepts into a unifying framework. The theoretical framework and practical tools of ecological stoichiometry (Tilman 1981, Sterner and Elser 2002) could be well suited for this purpose. Ecological stoichiometry considers how energy and elements are affected by and themselves affect organisms and their interactions in ecosystems (Allen and Gillooly 2009). As it happens, also this approach emerged from studies done in small lakes. Regardless of the theoretical framework, the present study (among many others) has confirmed that conceptual unambiguity and a thorough knowledge of the study system are the first prerequisites for theoretical development and for making appropriate observations. Conversely, any theory can be erroneously confirmed or refuted by misusing systems and misunderstanding concepts.

5 Acknowledgements

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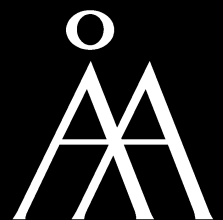
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