

Submerged macrophytes modify food web interactions and stability of lake littoral ecosystems

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Academic dissertation in environmental ecology

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ABSTRACT

Community structure and food web interactions determine ecosystem functioning and stability such as resistance to nutrient loading. Littoral habitats with submerged vegetation serve as major regulators of nutrient dynamics in lake ecosystems through habitat coupling. Deeper understanding of how trophic structure and biotic interactions within littoral communities are connected with water quality facilitates the designing of restoration measures for lakes suffering from eutrophy. The present study focuses on the structure and functioning of lake littoral ecosystems, especially plankton communities. Special interest is focused on the effects of submerged macrophytes in modifying food web interactions with respect to changes in planktivorous fish stocks and productivity. A series of enclosure and mesocosm experiments of factorial design were run in the littoral zone of Lake Vesijärvi, southern Finland, and also in five other lake littoral areas along a climatic gradient across Europe.

The results emphasised the general importance of consumer control over resource control in determining zooplankton community structures in shallow lake systems. Roach (*Rutilus rutilus* (L.)) preferred feeding on cladocerans even as they declined in abundance, while also using less-preferred, mainly non-animal food sources as alternative food. Thus, littoral subsidies stabilise planktivorous and omnivorous fish populations, which may intensify rather than dampen the strength of the interactions between fish and zooplankton. Plant-associated and small euplanktonic cladocerans, on the other hand, benefited from macrophytic refuge and could control phytoplankton when fish were not abundant (≤ 4 g fresh weight m^{-2} or ≤ 2.5 -4 ind. m^{-2}).

Community composition, primarily the abundance of submerged macrophytes and cladoceran grazers, played the decisive role in determining the stability of littoral ecosystems and resistance to nutrient enrichment, recorded as lower biomass of phytoplankton and periphyton. A macrophyte, *Elodea canadensis* Michx, hampered the growth and toxin production of cyanobacteria and regulated phytoplankton-zooplankton interactions. The mechanisms behind the control of phytoplankton growth by macrophytes were obviously complex and related to interactions and nutrient recycling within the food web, including heterotrophic processes. Wide year-to-year variation in littoral community composition, determined largely by prevailing weather conditions, resulted in variable outcome of perturbations imposed by nutrient loading. Such variable conditions may cause oscillations in the habitat coupling between littoral and pelagial zones through, for instance, variable recruitment and foraging behaviour of fish.

The phytoplankton biomass was positively related to the total phosphorus concentration even in the presence of efficient grazers, reflecting the positive response of adjacent trophic levels and the ultimate, quantitatively important role of productivity compared with consumer regulation in determining the phytoplankton biomass. However, the abundance of large crustacean grazers explained reasonably well the variance between productivity and algal biomass, even better than did the mere number of trophic levels. This result may be explained by factors such as heterogeneity within trophic levels and within the littoral habitat. The only consistent geographical pattern along the climatic gradient of Europe was the reduced role played by large crustacean grazers (> 0.5 mm) in controlling phytoplankton biomass in the southernmost location in Valencia, Spain, compared with the other sites. Although food web management appears to be a useful measure in northern temperate locations, nutrient control may be more important in southern lakes.

LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which in the text are referred to by their Roman numerals:

- I. Kornijów, R., Vakkilainen, K., Horppila, J., Luokkanen, E. & Kairesalo, T. 2005: Impacts of a submerged plant (*Elodea canadensis*) on interactions between roach (*Rutilus rutilus*) and its invertebrate prey communities in a lake littoral zone. *Freshwater Biology* 50: 262-276.
- II. Vakkilainen, K., Horppila, J., Väisänen, A., Sivonen, K. & Kairesalo, T. Submerged macrophytes increase the resistance of lake littoral to cyanobacterial blooming and toxin production after phosphorus enrichment. Manuscript.
- III. Hietala, J., Vakkilainen, K. & Kairesalo, T. 2004: Community resistance and change to nutrient enrichment and fish manipulation in a vegetated lake littoral. *Freshwater Biology* 49: 1525-1537.
- IV. Vakkilainen, K., Kairesalo, T., Hietala, J., Balayla, D., Bécares, E., Van de Bund, W., Van Donk, E., Fernández-Aláez, M., Gyllström, M., Hansson, L.-A., Miracle, M.R., Moss, B., Romo, S., Rueda, J. & Stephen, D. 2004: Response of zooplankton to nutrient enrichment and fish in shallow lakes: a pan-European mesocosm experiment. *Freshwater Biology* 49: 1619-1632.

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THE AUTHOR'S CONTRIBUTION

- I. KV, RK and EL set up the experiment and carried out field measurements and sampling. EL and KV planned the statistical analyses. KV analysed the zooplankton and phytoplankton samples, performed the data analyses, interpreted the results and drew the figures. KV wrote the paper in cooperation with TK and RK. RK and TK planned the experiment and TK supervised the work.
- II. TK, JHo and KV planned the experiment. KV wrote the paper, conducted data analyses and interpreted the results. TK supervised the work.
- III. JHi and KV took charge of setting up the experiments, field sampling and measurements. KV contributed to the laboratory measurements (excluding the nutrient analyses), analysed zooplankton samples, wrote and interpreted the zooplankton results, drew all the figures and contributed to the general discussion. TK supervised the work.
- IV. KV and JHi collected the data from the different laboratories and planned the data analyses. KV analysed the data, interpreted the results and wrote the paper. TK supervised the work.

In addition to the results of the original papers, the thesis also includes unpublished additional material analysed by the author.

ABBREVIATIONS AND CONCEPTS USED IN THE THESIS AND THEIR DEFINITIONS:

FW = fresh weight, synonym fresh mass used in papers III and IV

DW = dry weight, synonym dry mass used in papers III and IV

C = carbon, P = phosphorus, TP = total phosphorus, N = nitrogen

TSS = total suspended solids

chl *a* = chlorophyll *a*, algal photosynthetic pigment (Its concentration has been used as a surrogate of phytoplankton and periphyton biomass.)

euplanktonic = permanently planktonic species as opposed to plant-associated species living primarily on plant surfaces (cf. Hutchinson 1967)

edible and inedible algae for zooplankton = algal forms having the greatest axial length dimensions (GALD) of < 50 and ≥ 50 μm , respectively

DHM = diel horizontal migration, DVM = diel vertical migration

ANOVA = analysis of variance

1. INTRODUCTION

1.1 Aquatic ecosystem functioning

Role of trophic structure

Predicting how ecosystem functioning is determined by the trophic structure is one of the major challenges met in ecology (Jones & Lawton 1995, Polis & Winemiller 1996). In aquatic ecosystems, the discovery of the role played by predation in shaping zooplankton community structure with consequences on the efficiency of herbivory (Hrbáček *et al.* 1961, Brooks & Dodson 1965) inspired a number of studies on how the effects of higher trophic levels are reflected in the structure and biomass of lower trophic levels. Comparisons between lake ecosystems with differing food web length or manipulations of the top trophic levels showed evidence of the generally strong vertical structuring of aquatic food webs (e.g. Carpenter *et al.* 1985, Carpenter & Kitchell 1993, Salonen *et al.* 1990, Hansson 1992, Sarnelle 1992, Rask *et al.* 1996, Brett & Goldman 1997, Horppila *et al.* 1998, Jeppesen *et al.* 1998b, Järvinen & Salonen 1998). In general, the trophic structure of lake food webs can be defined as the partitioning of biomass into distinct trophic levels and is basically determined by available resources but is also regulated by dynamic feedback from higher trophic levels (Carpenter *et al.* 1985, Arditi & Ginzburg 1989, Power 1992, Carpenter & Kitchell 1993, Polis 1999). It is now well recognised that direct and indirect interactions within lake communities and food chain length may explain much of the variance in phytoplankton biomass that cannot be explained by variation in ecosystem productivity (Carpenter *et al.* 1985, Kerfoot & Sih 1987, Carpenter & Kitchell 1993, Sarvala *et al.* 1998).

The relative importance of resource and predator control in shaping community structure is viewed as complementary, not contradictory. For instance, the zooplankton community is expected to respond to changes both in available food resources and in predation pressure, reflecting the “sandwiched” role of zooplankton in aquatic food webs (Gliwicz 2002, Jeppesen *et al.* 2002a). However, the two forces operate on different time scales. The effect of predation is immediate, while it requires more time to transform enhanced productivity into new biomass, and this time lag is dependent on the generation time of organisms (Reynolds 1994, Gliwicz 2002). Therefore, the responses of the zooplankton community tend to be more vigorous to manipulations of fish than nutrients. Planktivorous fish keep the abundance of (large) herbivorous zooplankton, the intermediate consumer, at low levels and thus benefit prey living two trophic links lower, i.e. phytoplankton via reduced grazing and via enhanced nutrient regeneration (Carpenter *et al.* 1985). This trophic cascade from higher trophic levels can be traced back to the traditional food web hypothesis (Hairston *et al.* 1960, Fretwell 1977, Oksanen *et al.* 1981), which predicts that ecosystem productivity ultimately determines food chain length and that biomasses along the food chain exhibit discontinuous, alternating changes with productivity.

Even though the food chain models with their modifications (e.g. Scheffer 1991) have successfully explained much of the dynamics observed in aquatic ecosystems, these patterns may not always occur under natural conditions. Strong predator effects at the top of the food web (fish-zooplankton) are widely documented, while at lower trophic levels (zooplankton-phytoplankton) responses to fish manipulations are more variable across the productivity gradient (DeMelo

et al. 1992, Leibold *et al.* 1997). Increased productivity, on the other hand, often results in increased abundance of adjacent trophic levels and responses unrelated to the number of trophic levels in the food web (Arditi & Ginzburg 1989, Hansson 1992, Mazumder 1994, Brett & Goldman 1997, Leibold *et al.* 1997, Hansson *et al.* 1998b). Such variation was attributed to factors such as omnivory (Diehl & Feißel 2000), compensation or subsidized prey (Leibold *et al.* 1997, Pace *et al.* 1998), efficiency of consumers at exploiting their prey (Arditi & Ginzburg 1989, Power 1992, Abrams & Walters 1996) and habitat heterogeneity including refuges (Timms & Moss 1984, Persson *et al.* 1996). Trophic level heterogeneity has been addressed as one of the main limitations of simple food chain models, which are based on abstractions of the trophic levels represented, in effect, by a single keystone species (Osenberg & Mittelbach 1996, Leibold *et al.* 1997, Persson *et al.* 2001).

In aquatic ecosystems, large-bodied *Daphnia*, which are highly sensitive to fish predation, have generally been used as the keystone grazer and their abundance as a relevant indicator for predicting the grazing impact of zooplankton on phytoplankton (Hansson 1992, Sarnelle 1992, Cyr & Curtis 1999, Persson *et al.* 2001, Jeppesen *et al.* 2003). Zooplankton may also affect phytoplankton biomass via altered recycling of nutrients. Nutrient regeneration of planktonic animals is important especially in pelagic ecosystems (Järvinen & Salonen 1998, Hudson *et al.* 1999, Tarvainen *et al.* 2002, Vanni 2002). For example, *Daphnia* have a remarkably constant and low carbon-to-phosphorus (C:P) ratio compared with the higher variation in the seston C:P ratio and may therefore act as sinks for P by incorporating substantial amounts of P per body mass (Andersen & Hessen 1991, Salonen *et al.* 1994). However, there is so far little evidence for

the role of zooplankton-driven stoichiometry in changing phytoplankton biomass (Cyr & Curtis 1999). The relative importance of grazing and nutrient regeneration may often be difficult to interpret and is dependent on conditions such as time scale, lake depth and trophic state (Benndorf *et al.* 2002).

Aquatic ecosystem responses to nutrient enrichment

An increase in ecosystem productivity removes the nutrient constraints that tend to reduce the variation between predator-prey population interactions (DeAngelis *et al.* 1989). Nutrient enrichment may also lead to a succession toward invulnerable or predator-resistant prey such as filamentous or even toxic cyanobacteria, thus uncoupling the dynamics of zooplankton from the dynamics of phytoplankton (McQueen *et al.* 1986, Larsson & Dodson 1993, Abrams & Walters 1996). In general, however, efficient grazers reduce the sensitivity of phytoplankton biomass to nutrient enrichment (DeAngelis *et al.* 1989, Cottingham *et al.* 2004). Much ecological interest is focused on different stability properties of ecosystems with respect to their responses to perturbations, especially nutrient enrichment (reviewed in DeAngelis *et al.* 1989). Two central features of ecosystem stability include resistance, the ability of an ecosystem to resist perturbations, and resilience, the ability and the rate at which an ecosystem returns toward a steady-state equilibrium following perturbation (Carpenter *et al.* 1992, Wetzel 2001). Understanding of ecosystem responses to nutrient loading also has major implications for ecosystem management and restoration. Eutrophication due to nonpoint source loading of nutrients, especially P, continues to be one of the most widespread water quality problems and is

often difficult to manage and regulate (Wetzel 2001, Raıke *et al.* 2003).

Community structure plays a central role with respect to ecosystem responses to nutrient inputs (Carpenter *et al.* 1992, Jeppesen *et al.* 1998c). In addition, habitat heterogeneity together with flexible, adaptive behaviour of organisms may result in confounding effects that may interact with productivity, thus affecting community and ecosystem dynamics (Persson *et al.* 1996). Whole lake-scale experimentation has revealed uncertainties in predicting the functioning of lake ecosystems, thus suggesting drawbacks related to aquatic food web research, which has been carried out mainly in pelagic habitats. Planktivorous and omnivorous fish populations are stabilized by alternative food resources (subsidies) in the littoral ecosystem and may become uncoupled from the dynamics of zooplankton prey (Schindler & Scheuerell 2002). Switching of prey preference may reduce the predation pressure on zooplankton (Perrow *et al.* 1999) and thereby dampen their population fluctuations. However, anthropogenic disturbances, including eutrophication, alter habitat connections and thus the flows of nutrients and energy in lake ecosystems (Schindler & Scheuerell 2002).

1.2 Littoral ecosystems

Community structure in littoral habitats

Littoral habitats with submerged macrophytes and associated periphytic communities serve as important sinks for nutrients that enter the lake and as major regulators of nutrient dynamics in lake ecosystems through habitat coupling (Sarvala *et al.* 1982, Wetzel 1990, 2001, Wetzel & Sondergaard 1998, Schindler & Scheuerell 2002). Shallow lake areas lacking thermal stratification comprise

the majority of the earth's freshwater areas worldwide and therefore, in general, littoral areas overwhelmingly dominate the pelagic (Wetzel 1990). They are sensitive to eutrophication and resilient to management due to internal loading via effective exchange of nutrients between water and sediment. Resuspension may be an important process even in relatively deep lakes (Koski-Vahala *et al.* 2000) and sometimes more important than nutrient recycling by fish (Tarvainen *et al.* 2002). Abundant submerged vegetation reduces water movement and sediment resuspension and thus P regeneration (Horppila & Nurminen 2003). Nutrient regulation by macrophytes can be of the utmost importance in suppressing phytoplankton growth and cyanobacterial blooms during the growing season (reviewed in Sondergaard & Moss 1998). The existence of allelopathy also seems possible but has been a subject of ongoing debate, since its significance under field conditions is still too poorly evidenced (reviewed in Gross 2003). Furthermore, given the presence of macrophytes, changes in phytoplankton biomass throughout the growing season cannot be explained by allelopathy (Balayla & Moss 2004).

In addition to the proximity of bottom sediment, submerged vegetation creates a structurally rich habitat. It sustains a high diversity of different life forms from those attached to surfaces to those swimming or floating freely in the water column and to those exhibiting both of these ways of life. Thus, the structure as well as trophic interactions of macrophyte-associated littoral food webs are inherently complex (Kairesalo 1980, Scheffer *et al.* 1993, Kornijow & Kairesalo 1994, Jeppesen *et al.* 1998c, Scheffer 1999) (Fig. 1). High habitat structural complexity increases the spatial separation and availability of refuges thus limiting populations, influencing consumer-resource dynamics and weakening the strength of trophic

cascades through foraging efficiency of predators (Persson *et al.* 1996, Polis *et al.* 2000, Shurin *et al.* 2002). For instance, the foraging ability of roach *Rutilus rutilus* (L.) decreases with habitat complexity and macrophyte coverage (Persson 1987, Diehl 1993, Moss *et al.* 1998). One of the fascinating roles of submerged macrophytes is their potential for providing refuge for zooplankton against fish predation, thus hampering the trophic cascade (Timms & Moss 1984, Carpenter *et al.* 1985, Lauridsen *et al.* 1996, Jeppesen *et al.* 1998a, Kairesalo *et al.* 1998, 2000, Scheffer 1999).

Relative roles of macrophytes and zooplankton in controlling phytoplankton biomass

In plant beds, both euplanktonic and littoral, plant-associated cladoceran species may occur in dense swarms and play an important role in controlling phytoplankton biomass (Kairesalo 1980, Walls *et al.* 1990, Jeppesen *et al.* 1998c, 1999, Nurminen *et al.* 2001, Balayla & Moss 2004). Zooplankton grazing, especially that of *Daphnia*, is of central importance in enhancing water clarity and the availability of light for macrophytes. On the other hand, several studies reported negative effects of submerged macrophytes on zooplankton, especially

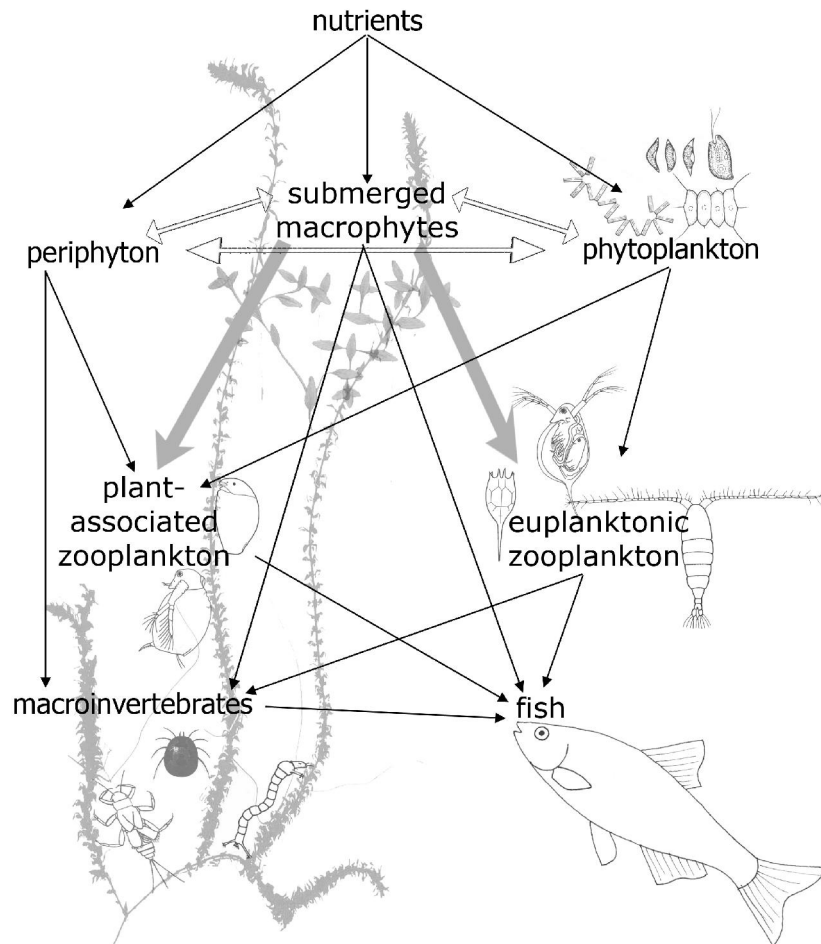


Figure 1. Schematic overview of interactions between different constituents of a littoral food web. The arrows show the processes of interest in this thesis. Food web links are illustrated by thin black arrows and spatial refuge by broader grey arrows, while resource competition and allelopathic interactions are illustrated by open arrows. (Modified from Van Donk & Van de Bund 2002.)

Daphnia, due to low food supply, high daytime pH, low-oxygen conditions, invertebrate predation or plant chemicals (Hasler & Jones 1949, Pennak 1973, Kairesalo 1980, Dorgelo & Heykoop 1985, Jeppesen *et al.* 1998a, Blindow *et al.* 2000, Burks *et al.* 2000, 2002). Littoral phytoplankton may be low in biomass (Schriver *et al.* 1995) or in quality (Kairesalo 1980, Smiley & Tessier 1998) compared with pelagic phytoplankton.

In contrast, other studies have revealed that small mobile flagellates with high growth rates appear successful in the presence of macrophytes and serve as high-quality food for zooplankton (Søndergaard & Moss 1998). Zooplankton, including *Daphnia*, may also use alternative food sources in the littoral zone by browsing on plant, sediment and other surfaces (Horton *et al.* 1979, Jeppesen *et al.* 2002b). In addition, macrophyte beds may be rich in bacteria that can be utilized as food by many cladoceran species (Søndergaard *et al.* 1998). Factors such as species, density and the growth phase of macrophytes also affect conditions in the vegetation and its quality as habitats for zooplankton. By migrating horizontally or vertically between open-water habitats or sediment surface and macrophyte beds, cladocerans may avoid constant susceptibility to the possible adverse effects of macrophytes while still benefiting from the refuge (Timms & Moss 1984, Walls *et al.* 1990, Lauridsen *et al.* 1996, Smiley & Tessier 1998, Burks *et al.* 2002, Jeppesen *et al.* 2002b).

Macrophytes may also modify fish-zooplankton interactions through sustaining a habitat with multiple alternative food sources for fish (Persson 1987, Diehl 1993, Moss *et al.* 1998, Perrow *et al.* 1999, Schindler & Scheuerell 2002). Generalist feeding behaviour, i.e. switching of prey preference, may reduce the predation pressure on zooplankton (Perrow *et al.*

1999) and thereby dampen their population fluctuations. On the other hand, it was suggested that such behavioural flexibility may have only a short-term stabilizing effect, depending on the predator's behaviour and food preferences (Murdoch & Bence 1987). For instance, in the littoral zone of Lake Vesijärvi, southern Finland, the percentage share of zooplankton in the diets of roach decreases and the proportion of benthos and macrophytes increases with the low availability of planktonic food (Horppila & Kairesalo 1992) and with the increasing size of fish (Horppila 1994). However, the consequences of such plasticity in food preference for zooplankton-phytoplankton interactions and for functioning of the littoral ecosystem have been less quantified (reviewed in Jeppesen *et al.* 1998c).

The spatial heterogeneity produced by submerged vegetation, coupled with the movement of organisms between open-water, vegetated and benthic environments may provide important compensatory mechanisms. They work as a buffering mechanism in shallow lakes and littoral ecosystems, where the outcome of perturbation, such as nutrient loading, results from variable responses of organisms from different habitats that may partially or completely compensate for, or strengthen, each other's effect (Scheffer *et al.* 1993, Jeppesen *et al.* 1998c, Scheffer 1999). Thus, it may be difficult to estimate the relative importance of macrophytes and fish predation in structuring the littoral invertebrate community (Jeppesen *et al.* 1998c). The structuring role of submerged macrophytes in controlling phytoplankton growth is generally acknowledged, although the mechanisms behind this phenomenon are still arguable and partly contradictory (cf. Jeppesen *et al.* 1998c, 1999). The debate stems from the ultimate complexity of macrophyte-related mechanisms and differences in

their relative role, which may vary with lake morphometry, plant community composition, trophic state of the lake as well as climate (Jeppesen *et al.* 1999, Scheffer *et al.* 2001).

1.3 Ecosystem regime shifts

Natural populations always fluctuate, even when factors such as seasonality or climatic variation are disregarded. Multiple variables changing at different rates with different directions of feedbacks were attributed to catastrophic regime shifts in ecosystems (Scheffer & Carpenter 2003). These shifts are variable and are dependent on several factors such as lake morphometry, temperature and the predominance of macrophytes (Genkai-Kato & Carpenter 2005). Shallow lakes provide among the best-documented regime shifts, so called alternative stable states, with either a turbid, phytoplankton-dominated state or a clear-water, plant-dominated state, depending on their community structure, through complex feedback mechanisms (Irvine *et al.* 1989, Scheffer *et al.* 1993, cf. Chapter 1.2). In deep stratified lakes, alternative stable states were related to P recycling by fish and/or from anoxic sediments (Carpenter *et al.* 1992, Horppila *et al.* 1998, Genkai-Kato & Carpenter 2005). On the other hand, the existence of real, sustained alternative stable states in lake ecosystems has been debated (Sarvala *et al.* 2000, Van de Bund & Van Donk 2002).

Macrophyte-dominated ecosystems may not be affected by ongoing eutrophication until a threshold is reached at which a large switch, or regime shift, occurs leading to a takeover by phytoplankton (Scheffer *et al.* 1993, Scheffer & Carpenter 2003, Folke *et al.* 2004). Algal blooms hamper macrophytic growth through shading and gain advantage over nutrient regeneration via sediment resuspension. Trophic cascades

further increase the vulnerability of the ecosystem to nutrient input and are typically manifested by the loss of top predators, i.e. piscivorous fish, leading to a resilient system with abundant planktivores, small-bodied zooplankton and abundant phytoplankton (reviewed in Folke *et al.* 2004). Mere reduction in external nutrient loading may not be sufficient to lead to the recovery of macrophytes and revert a turbid lake to a clear-water state but major perturbations, such as fish manipulation, are needed to decrease internal nutrient loading (Scheffer *et al.* 1993, Moss *et al.* 1996, Horppila *et al.* 1998, Mehner *et al.* 2002).

Such ecosystem resilience has been a matter of extensive interest, because these alternative stable states can also be used as a conceptual basis for successfully managing shallow lake ecosystems (Moss *et al.* 1996, Mehner *et al.* 2002). Indeed, restoration of eutrophicated, turbid lakes has been most successful in shallow lakes, where macrophytes can colonise large bottom areas, thus increasing the resistance to nutrient loading (Mehner *et al.* 2002). However, techniques for restoration have been developed largely in northern temperate locations, while it is less clear how efficiently measures such as manipulation of the fish community may operate at lower latitudes (Stephen *et al.* 2004).

1.4 Changes in the functioning of shallow aquatic ecosystems with climate

All biochemical and biological processes such as population cycles, biomass turnover times and trophic interactions have rates of operation that are temperature-dependent (McCauley & Murdoch 1987, Lehman 1988, Petchey *et al.* 1999). Such factors are likely to affect communities, especially in shallow aquatic ecosystems (cf. Hargeby *et al.*

2004). Increasing temperature may facilitate the recolonisation of macrophytes in shallow lakes, depending on the efficiency of zooplankton at producing clear-water phases (Scheffer *et al.* 2001). It may also induce lakes to be more susceptible to nutrient loading (Genkai-Kato & Carpenter 2005).

Production of zooplankton increases with temperature, while biomass accumulation is more dependent on resource availability (Shuter & Ing 1997). Similarly, enhanced primary productivity at higher temperatures (cf. Petchey *et al.* 1999) becomes more controlled by nutrient turnover rate and availability. Accordingly, with rising temperature the inherently faster growth rate of algae compared with that of zooplankton may lead to reduced control of algal biomass by zooplankton. In addition, the threshold food level of zooplankton increases with water temperature and, for metabolic reasons, with increasing animal size (Lehman 1988). The available evidence suggests that the size structure of zooplankton assemblages shifts from large-bodied (efficient) grazers toward smaller (less efficient) grazers (Moore *et al.* 1996). Fish predation may further suppress large zooplankton since the activity and capture success of several planktivorous fish, such as roach, increase with temperature (Persson 1986). With increasing temperature, effects at the resource base may play a major role in the functioning of food webs, while the cascading effects of fish via zooplankton grazers could play a minor role in controlling algal biomass. Thus, in southern locations manipulation of the fish community may not be as appropriate a technique for lake restoration as in northern temperate locations.

1.5 Fish stock management, an efficient restoration measure in Lake Vesijärvi, southern Finland – implications for fish-mediated habitat coupling

In Lake Vesijärvi, cultural eutrophication due to industrial and domestic waste water began in the early 20th century and was manifested by massive cyanobacterial blooms that persisted even after sewage diversion (Keto & Sammalkorpi 1988). In the early 1990s, the cyanobacterial blooms suddenly disappeared and water clarity markedly increased following the drastic decrease of external loading and a five-year mass removal of fish, mainly roach and smelt *Osmerus eperlanus* (L.) from 172 kg ha⁻¹ to less than 30 kg ha⁻¹ (Horppila *et al.* 1998, Kairesalo *et al.* 1999). A new increase in planktivorous fish in the pelagic zone was prevented by continued management fishing and stocking of predatory fish, especially pikeperch *Sander lucioperca* (L.), (Kairesalo *et al.* 1999, Ruuhijärvi *et al.* 2005).

The decline in the ecosystem productivity, including reduced internal loading and transport of P from the littoral zone by roach rather than reduced planktivory and enhanced herbivory were considered the decisive factors in the decline of cyanobacteria and in shifting the lake ecosystem into the clear-water state (Horppila *et al.* 1998, Kairesalo *et al.* 1999). The appearance of cyanobacteria in highly productive lakes often cannot be explained based on a simple herbivore-phytoplankton interaction (reviewed in Persson *et al.* 1996). Cyanobacteria tend to inhibit zooplankton feeding due to their colonial morphology through mechanical interference and/or direct toxicity, with consequences for the growth of zooplankton, especially *Daphnia* (Lampert 1987, Hietala *et al.* 1995). After the disappearance of cyanobacteria in

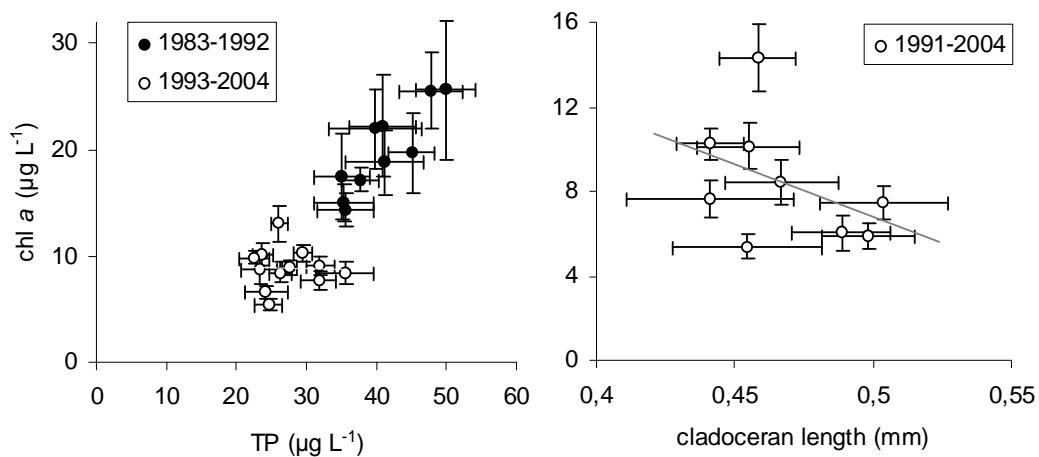


Figure 2. Relationship between epilimnetic chlorophyll *a* (chl *a*) and (a) total phosphorus (TP) concentrations and (b) cladoceran mean body length (May-September means \pm 1 SE) in the Enonselkä Basin of Lake Vesijärvi. Note the different scales of chl *a* concentrations.

Lake Vesijärvi, the phytoplankton biomass was dominated by more edible algal forms such as cryptophytes and diatoms (Keto & Tallberg 2000). Low deviation in chlorophyll *a* (chl *a*), despite a relatively wide variation in P concentrations, suggest enhanced control of phytoplankton biomass by grazing compared with the situation before the lake shifted to its present state (Fig. 2) (Kairesalo & Vakkilainen 2004). An inverse relationship also prevailed between chl *a* concentration and cladoceran body length (Fig. 2) but not

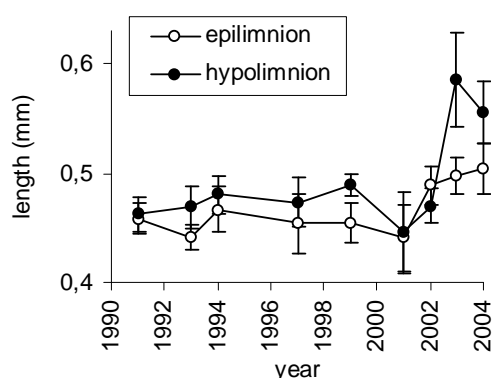


Figure 3. Density-weighted body length (growing season means \pm 1 SE) of cladocerans in the epilimnion (0-10 m) and hypolimnion (10-29 m) of the Enonselkä Basin, Lake Vesijärvi in 1999-2004.

biomass (Vakkilainen *et al.* unpublished data). Cladoceran body length is an important predictor of phytoplankton biomass and water clarity (Carpenter *et al.* 1998, Stemberger & Miller 2003, but see Sarvala *et al.* 1998) as well as a surrogate of size-selective predation and planktivorous fish abundance (Soranno *et al.* 1993). In Lake Vesijärvi, the body length of the cladoceran community remained remarkably stable during the 1990s, reflecting negligible changes in planktivorous fish stocks during that period. In the early 21st century, the body length increased (Fig. 3) with changes in the relative abundances of species (Vakkilainen & Kairesalo 2005). This coincided with the intensified fishery management initiated in 2000 and with the collapse of the smelt stock in 2002-2003 (Ruuhijärvi *et al.* 2005). Such changes in the food web structure were attributed to relatively high transparency coinciding with a deficiency in hypolimnetic oxygen even at 7-10-m depths, i.e. at euphotic zone, in late summers 2002 and 2003 (Fig. 4). The decreased hypolimnetic water volume available for zooplankton to hide from planktivorous fish may partly explain the concomitant drastic reduction in

cladoceran biomass from ca. 190 to 80 $\mu\text{g C l}^{-1}$ within two weeks in both 2002 and 2003 (Vakkilainen *et al.*, unpublished data). With high increasing transparency the risk of predation may increase despite of potentially low share of planktivorous fish, in accordance with conclusions by Jeppesen *et al.* (2003). These phenomena in Lake Vesijärvi were accompanied by incidental late summer blooms of cyanobacteria in 2002 and 2003. During the rainy and windy summer 2004, oxygen conditions were improved (Fig. 4) and no algal blooms were recorded.

Before the restoration of Lake Vesijärvi, the maximum depth of submerged vegetation was 2 m but thereafter macrophytes colonised the bottom down to 4-m depth (Venetvaara & Lammi 1995). In the Enonselkä Basin, the potential area for the growth of submerged macrophytes increased from ca. 4.8 km^2 to 8.5 km^2 . Such structural changes within the littoral areas also suggested altered regulation of nutrients and food web dynamics. Both roach and perch *Perca fluviatilis* (L.) effectively utilise different habitats and diverse food resources in Lake Vesijärvi (Horppila *et al.* 2000) and thus littoral and benthic

resources are an important subsidy for fish populations (Horppila *et al.* 1998, Kairesalo *et al.* 1999, cf. Schindler & Scheuerell 2002, Vadeboncoeur *et al.* 2002). Differential use of habitats by fish may be an important factor affecting water quality (Holopainen *et al.* 1992, Horppila *et al.* 1998). Wide variation in the recruitment of roach in Lake Vesijärvi suggested the presence of variable conditions in the littoral zone (Horppila *et al.* 1998). Similar observations were done in a number of other lakes, suggesting the major importance of littoral and benthic factors such as submerged macrophytes and benthic feeding fish in affecting the outcome of food web restoration of eutrophic lakes (Hansson *et al.* 1998a). Considerations of lake restoration through food web management, which formerly focused primarily on pelagic food chains, i.e. phytoplankton-zooplankton-fish interactions (Carpenter *et al.* 1985, Carpenter & Kitchell 1993, Reynolds 1994, Moss *et al.* 1996), have now gone forward in attempts to integrate whole-lake ecosystem processes (Hansson *et al.* 1998a, Schindler & Scheuerell 2002, Vadeboncoeur *et al.* 2002).

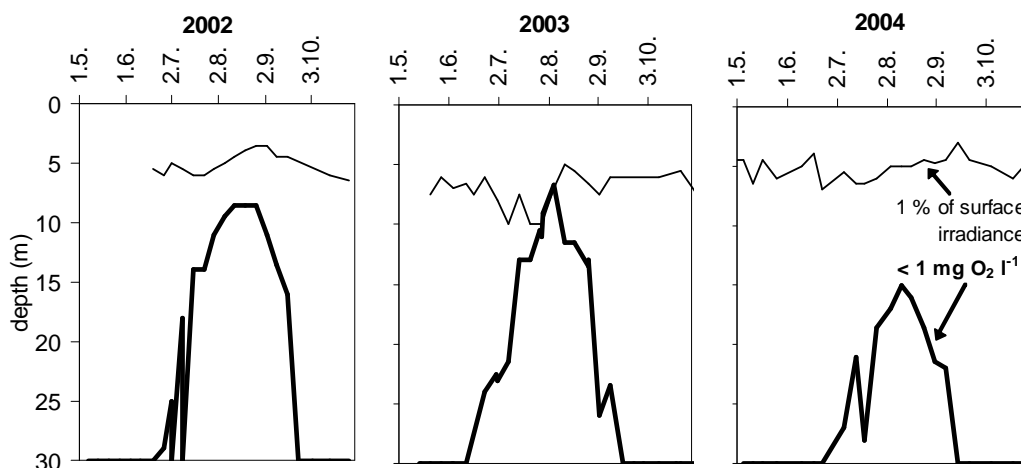


Figure 4. Compensation depth (1 % of surface irradiance, measured with a LiCor LI-1400 4π sensor) and the depth of oxygen deficient hypolimnetic water ($< 1 \text{ mg O}_2 \text{ l}^{-1}$) of the Enonselkä Basin, lake Vesijärvi during the growing season in 2002, 2003 and 2004.

2. OBJECTIVES OF THE PRESENT STUDY

Alterations in planktonic food webs following fish manipulation trigger other, mainly benthic and littoral, processes in lakes (Hansson *et al.* 1998a). However, compared with extensive studies in the pelagic zone of lakes, trophic interactions within the littoral zone are less well explored (cf. Jeppesen *et al.* 1998c). From a practical point of view, deeper understanding of how the trophic structure and biotic interactions within the littoral community are connected with water quality facilitates the designing of proper restoration measures. Moreover, they may play a crucial role in the stability of the improved state after restoration. The zooplankton-phytoplankton link is affected by several confounding factors such as variation in nutrients, climate, algal edibility and macrophytic vegetation, which have been the subjects addressed in controlled experiments to identify underlying mechanisms (e.g. DeMelo *et al.* 1992, Jeppesen *et al.* 1998c).

The present study focuses on the structure and functioning of the littoral community. Special interest is focused on the effects of submerged macrophytes in modifying food web interactions with respect to changes in planktivorous fish stocks and productivity (Fig. 1). Generalist feeding behaviour and switching of prey preference by fish as well as macrophytic refuges for zooplankton against fish predation are expected to have major implications for the dynamics of littoral predator-prey interactions. The submerged vegetation with its associated biota can be assumed to increase the resistance of the littoral ecosystem to nutrient loading, while contrasting effects are expected with the increasing abundance of planktivorous fish. Given the major role of nutrient availability in the functioning of food webs at low latitudes, the cascading

effects of fish via zooplankton grazers are expected to increase with increasing latitude.

The main questions addressed in this thesis are:

1. Do submerged macrophytes modify the structure and functioning of the littoral community through providing zooplankton with a refuge against fish predation and a habitat rich in alternative food sources for omnivorous fish, thus changing the cascading effects of fish via zooplankton grazers?
2. Do submerged macrophytes increase lake littoral resistance and resilience to nutrient enrichment?
3. How much is the resistance of the littoral ecosystem against nutrient enrichment modified by fish, especially through cascading impacts via zooplankton, and does the relative importance of resource availability and predation change along with different climatic conditions?

Mesocosms are laboratory or field enclosures, i.e. enclosed sub-systems that can be controlled and replicated. Mesocosm experiments are a powerful experimental tool for studying ecological mechanisms such as planktonic food web interactions and chemical effects up to a few months in duration (Schindler 1990, Carpenter & Kitchell 1993). This was the approach used in this thesis. Thus, the functioning of the littoral ecosystem was studied by conducting series of controlled field mesocosm experiments of factorial design to answer the above questions.

3. MATERIAL AND METHODS

3.1 Study sites

The field experiments were performed at 1.0-1.7-meter water depth in shallow lakes or lake littoral zones. The main study site (I-IV) was situated in the shallow Kilpiäistenpohja Bay (water depth < 3 m), which lies adjacent to the Enonselkä Basin of Lake Vesijärvi, southern Finland (Table 1, Fig. 5).

Kilpiäistenpohja Bay is characterised by abundant submerged vegetation, mainly *Elodea canadensis* Michx., *Myriophyllum* spp. and *Ceratophyllum demersum* L., covering large areas of the bottom of the open water area together with floating-leaved macrophytes, e.g. *Nuphar lutea* L. (Fig. 5). Freely floating *Lemna trisulca* L. is a characteristic species in the bay and forms thick flocks through the entire water column. The emergent vegetation is dominated by *Phragmites australis* (Cav.) Trin. ex Steud. Roach and perch are the

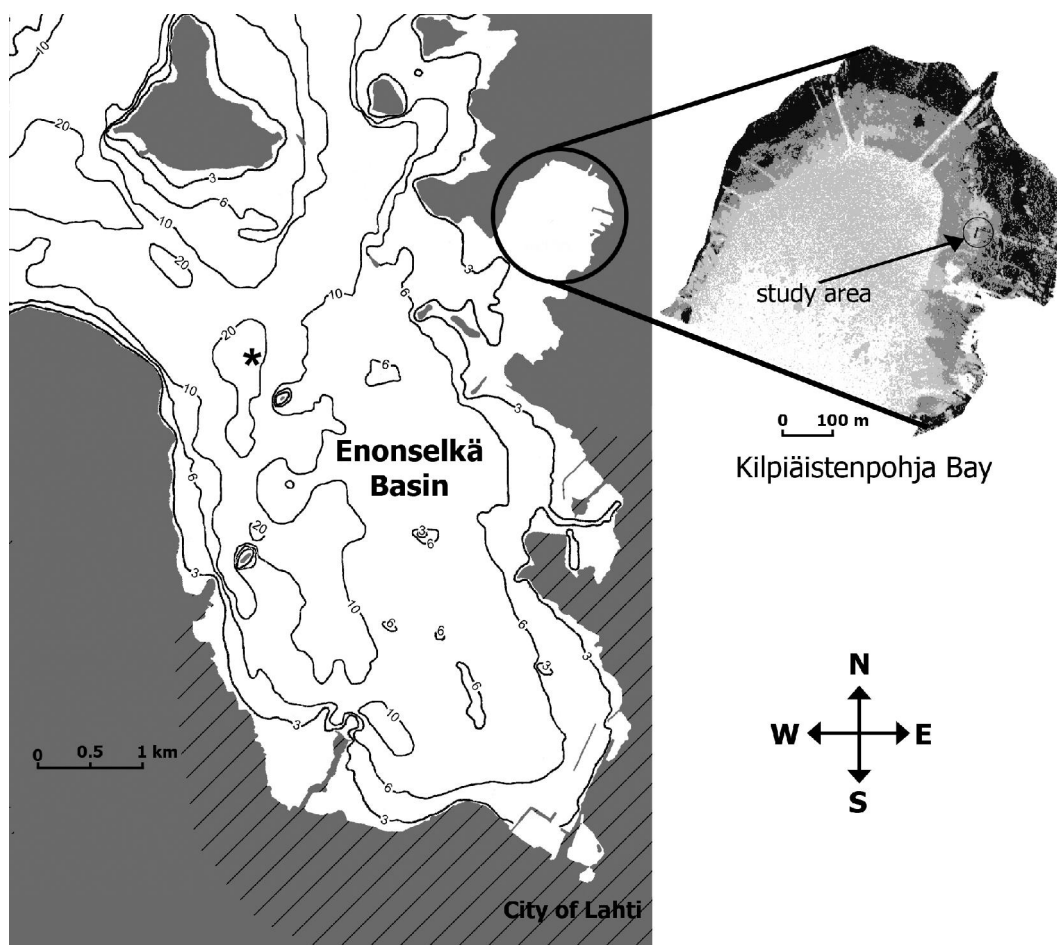


Figure 5. The bathymetric map of the Enonselkä Basin of Lake Vesijärvi showing the location of Kilpiäistenpohja Bay as well as the sampling point (denoted by an asterisk), where long-term water quality and plankton monitoring have been conducted (Chapter 1.5). The striped area denotes the urban, mainly built areas of the City of Lahti. The magnification of the Kilpiäistenpohja Bay (right) shows the location of the main study area. It also illustrates the different vegetation zones identified from an aerial photo (Copyright FM-Kartta Oy) using optical resolution parameters. The zones are interpreted as follows: black = emergent vegetation, dark grey = floating-leaved vegetation, light grey = submerged vegetation, white = no identified vegetation.

most abundant fish species in the littoral area (Kairesalo *et al.* 1999, Horppila *et al.* 2000). The biomass of northern pike *Esox lucius* (L.) decreased with eutrophication (Keto & Sammalkorpi 1988) but has since increased due to stocking of pike fingerlings. Since 1997, yearly pike catches in Lake Vesijärvi have averaged 1.5 kg ha⁻¹ (Ruuhijärvi *et al.* 2005).

The other study sites (IV) were situated across Europe in Sweden, England, The Netherlands, northern Spain (Leon) and southern Spain (Valencia) (Fig. 6) and were chosen to represent shallow mesotrophic-hypertrophic lakes in which submerged vegetation had been abundant during the years immediately preceding the experiments (Table 1).



Figure 6. Map showing the locations of the field experiments along the European climatic gradient.

Table 1. General characteristics of the study lakes.

Lake	Location	pH	TP ($\mu\text{g L}^{-1}$)	Dominant submerged macrophyte taxa
Vesijärvi	Finland 61°02' N, 25°39' E	7.5- 7.9	30-60	<i>Lemna trisulca</i> L., <i>Elodea canadensis</i> Michx., <i>Myriophyllum</i> spp., <i>Ceratophyllum demersum</i> L.
Krankesjön	Sweden 55°42' N, 28°19' E	8.2	25	<i>Myriophyllum</i> spp., <i>Chara</i> spp.
Little Mere	England 53°20' N, 2°24' E	7.3	184	<i>Potamogeton berchtoldii</i> Fieber, <i>Elodea canadensis</i> , <i>Ceratophyllum demersum</i>
Naardemeer	the Netherlands 52°30' N, 5°01' E	8.5- 9.6	30	<i>Chara</i> spp.
Sentiz	Leon, northern Spain 42°33' N, 5°22' E	8.4- 9.0	100	<i>Myriophyllum alterniflorum</i> L.
Xeresa	Valencia, southern Spain 39°6' N, 0°20' E	8.7- 8.9	17-22	<i>Chara</i> spp.

3.2 Design of the experiments

All the experiments had fully factorial design with two factors and aimed at studying the littoral community responses to a submerged macrophyte *Elodea canadensis* (I, II), planktivorous fish (I, III, IV), weekly P and nitrogen (N) enrichment (III, IV) or P enrichments conducted either once at the beginning of the experiment (pulse enrichment) or weekly (press enrichment) (II) (Table 2). The experiments were conducted in 1994 and 1996 in rectangular enclosures of 2 x 2.5 m (I, II) or in 1998 and 1999 in

cylindrical mesocosms of 1-m diameter (III, IV) (Table 2). In 1998 and 1999, the experiments were conducted concomitantly in the different study sites along the European climatic gradient (Fig. 6). Thus, twelve parallel experiments (collectively the International Mesocosm Experiment, IME) were carried out in order to study large-scale between-year variation in the effects of planktivorous fish and nutrient enrichment on littoral communities (Stephen *et al.* 2004). Inevitably, the fish species differed between locations but, however, taxon is considered less

Table 2. Summary of the experimental designs. Hereafter, in the text the treatments are referred to as denoted in this table.

Time of experiment and size of mesocosms	Treatment 1 (levels in brackets)	Treatment 2 (levels in brackets)	No. of replicates	Paper
1-29 August, 1994 ⁽¹⁾ (4 weeks) area 5 m ² vol. 7.5 m ³	4-5-year-old (16 cm) roach: no-fish = 0 g FW m ⁻² high-fish = 69 g FW m ⁻² (1.9 ind. m ⁻²)	<i>Elodea canadensis</i> : no- <i>Elodea</i> = 0 g DW m ⁻² sparse- <i>Elodea</i> = 17.5 g DW m ⁻² , dense- <i>Elodea</i> = 52.5 g DW m ⁻²	3	I
25 June – 31 July, 1996 (5 weeks) area 5 m ² vol. 7.5 m ³	Phosphorus: control = 0 mg P l ⁻¹ pulse = one initial P enrichment of 0.04 mg P l ⁻¹ press = five weekly P enrichments of 0.04 mg P l ⁻¹	<i>Elodea canadensis</i> : no- <i>Elodea</i> = 0 g DW m ⁻² <i>Elodea</i> = 105 g DW m ⁻²	3	II
8 June – 13 July, 1998 (5 weeks; III) or 8 June – 20 July, 1998 (6 weeks; IV) area 0.8 m ² vol. 0.7-1.0 m ³	Weekly nutrient enrichments: (0 mg P + 0 mg N l ⁻¹ , 0.1 mg P + 1 mg N l ⁻¹ , 0.5 mg P + 5 mg N l ⁻¹ , 1.0 mg P + 10 mg N l ⁻¹)	Locally appropriate planktivorous fish species of 5-10-cm length ⁽²⁾ : fish-free = 0 g FW m ⁻² low-fish = 4 g FW m ⁻² (2.5-4 ind. m ⁻²) high-fish = 20 g FW m ⁻² (7-20 ind. m ⁻²)	3	III, IV
29 June – 10 August, 1999 (7 weeks; III) or 29 June – 4 August, 1999 (6 weeks; IV) area 0.8 m ² vol. 0.7-1.0 m ³	Weekly nutrient enrichments: (0 mg P + 0 mg N l ⁻¹ , 0.03 mg P + 0.3 mg N l ⁻¹ , 0.06 mg P + 0.6 mg N l ⁻¹ , 0.09 mg P + 0.9 mg N l ⁻¹ , 0.15 mg P + 1.5 mg N l ⁻¹ , 0.30 mg P + 3.0 mg N l ⁻¹)	Locally appropriate planktivorous fish species of 5-10 cm length ⁽³⁾ : fish-free = 0 g FW m ⁻² low-fish = 4 g FW m ⁻² (2.5-4 ind. m ⁻²) high-fish = 20 g FW m ⁻² (7-20 ind. m ⁻²)	2	III, IV

⁽¹⁾ The enclosures were set up two weeks before the fish manipulation, on 14 July, to allow them to recover from disturbance.

^(2,3) In the experiment conducted in Lake Vesijärvi, 6-9-cm juvenile roach⁽²⁾ and 8-10-cm juvenile perch⁽³⁾ were used.

determinative than biomass or size with respect to zooplanktivory (Williams & Moss 2003). Compromises about the most appropriate nutrient enrichment levels across locations were less easy to make and drawbacks could not be avoided. During the third week of the experiment in 1998 in Finland, high fish mortality occurred at the two highest nutrient levels, probably due to the high pH (> 9) of the water. Therefore, the results of these nutrient treatments were excluded from the data analyses and the nutrient range was narrowed in 1999 (Table 2). This and other accidental events, such as the break-up of the Swedish experiment in windy summer 1998, resulted in the exclusion of some data, described in more detail in paper IV.

The mesocosms, made of watertight, clear polyethylene (PE) plastic, were open to the atmosphere and the low ends were sealed into the lake bottom sediment so that the water was in contact with the sediment. The experimental area was covered with a net to prevent the entry of birds. The fish and macrophytes used in the experiments were collected from a nearby lake area.

3.3 Sampling procedure, sample and data analyses

Samples for water chemistry, chl *a*, phytoplankton, zooplankton, microcystins (only in 1996; II) and total suspended solids (TSS; only in 1998) were collected weekly at 9-11 a.m. with a transparent Perspex core (length 1.5 m, inner diameter 4.0-4.5 cm) from the surface to the bottom of each enclosure. Special care was taken not to disturb the sediment. A total of 5-10 subsamples were taken from different places of the mesocosms, pooled and mixed. In a similar way, additional samples were taken weekly also from the lake outside the enclosures in 1994, 1998 and 1999.

The first samples were taken just before the introduction of fish and/or first nutrient addition. The short-term impact of *Elodea* on roach-zooplankton interaction was studied in 1994 by taking an additional set of samples three days after the introduction of roach (I). On 28-29 June, 1998, three weeks after the onset of the experiment, samples were also taken between 11 p.m. and 1 a.m. to examine the possible daytime aggregation of *Daphnia* and other crustacean zooplankton close to the sediment, as well as their diel vertical migration (DVM). Concomitantly with the sampling procedure, the temperature, oxygen and secchi depth were measured in the field. On the last week of the experiment in 1999, vertical profile of light penetration into water was measured also with a LiCor LI-1400 4 π sensor (Li-Cor Ltd., Lincoln, NE, U.S.A.). The standard methods used in physical and chemical determinations, microscopic plankton analyses as well as data analyses are described in detail in each individual paper.

Samples for TSS (additional results in this thesis) were filtered through dried (105°C), weighed Whatman GF/F filters (Whatman International, Maidstone, UK). After drying (105°C, 2 hours), the filters were weighed for the amount of TSS. On 4-5 August, 1999, samples of epiphytic macroinvertebrates (additional results in this thesis) were taken from macrophyte beds of each enclosure using a core sampler (length 32 cm, diameter 13 cm; Kornijów 1998). Living animals were identified, weighed and their biomass was calculated per macrophytic biomass.

The additional time series results presented in this thesis were analysed using repeated mixed procedure of the SAS package, version 6.12 (Statistical System Institute Inc., USA). Further information about the mixed model is given in papers I and II. Other statistical tests were done using univariate analysis of variance (ANOVA, followed by

Tukey's test) or Pearson's bivariate correlation test of SPSS for Windows (version 10.0). When the assumptions for ANOVA were not met, log transformation was used to stabilize heterogeneous variances or to normalize the distribution of residuals.

4. RESULTS AND DISCUSSION

4.1 Fish-zooplankton interactions within macrophyte beds

In shallow lakes and littoral zones, edge zones between plant beds and open water as refuges for *Daphnia* were considered an important buffering mechanism to changes in fish predation pressure (Schriver *et al.* 1995, Lauridsen *et al.* 1996, Jeppesen *et al.* 1998a, Moss *et al.* 1998). Consequently, during a 3-day period after roach introduction the biomass of *Daphnia longispina* O. F Müller was reduced more in the no-*Elodea* enclosures than in the *Elodea* enclosures (I). However, *Elodea* also had a strong negative impact on *Daphnia*, thus complicating the estimation of the refuge effect (I; Fig. 1). In another

experiment without fish treatments in 1996, no negative effects of *Elodea* on *Daphnia* were evident (II). Burks *et al.* (2000) demonstrated that the growth of *Daphnia magna* Straus was strongly suppressed when exposed to chemicals from both *E. canadensis* and roach. Schriver *et al.* (1995) found positive effects of macrophytes but a negative interaction of fish and macrophytes on zooplankton biomass. Chemical communication plays a major role in aquatic habitats (Larsson & Dodson 1993, Burks *et al.* 2002, Gross 2003) and the responses of plankton to different combinations of numerous chemical signals may be multifaceted especially in littoral habitats (Larsson & Dodson 1993). Such communication may become pronounced in enclosed systems that do not allow large-scale horizontal migration of *Daphnia* (I) (cf. Burks *et al.* 2002). The repellent properties of macrophytes on *Daphnia* and other zooplankton (Hasler & Jones 1949, Pennak 1973, Dorgelo & Heykoop 1985, Blindow *et al.* 2000, Burks *et al.* 2000, 2002) are certainly dependent on variable conditions within plant beds and one of the key factors appears to be the presence of fish.

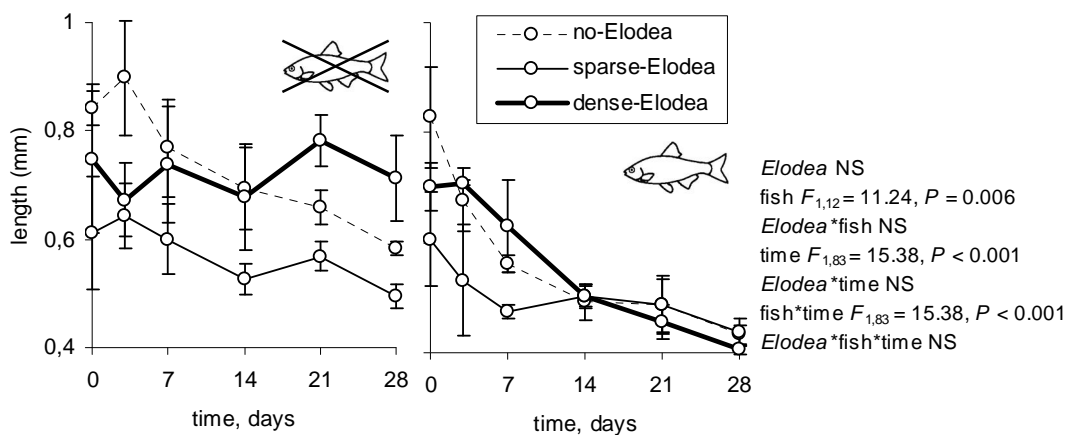


Figure 7. Treatment means (+ 1 SE) over the course of the experiment for the body length of euplanktonic cladocerans in the *Elodea* enclosures with or without fish (I). The F ratios with significance levels for the main effects and interactions of *Elodea*, fish and time obtained in the mixed model are given for each variable.

Fish introduction generally led to the reduction in large-bodied, filter-feeding cladoceran biomass, especially *Daphnia*, which became virtually absent with fish regardless of the abundance of macrophytes (I, III, IV). This result addresses the generally high predation risk in shallow lakes (Jeppesen *et al.* 2003) also suggested by the negligible numbers of daphnids in the open lake area outside enclosures (0-5 ind. l⁻¹; unpublished data) and their notable increase when enclosed and protected from fish predation (I, II). The ineffectiveness of the *Elodea* refuge was also evidenced by the equally decreasing body size of euplanktonic cladocerans in all *Elodea* treatments with 16-cm roach (Fig. 7) (I). In contrast, small cladocerans such as *Ceriodaphnia*, a genus well adapted to plant beds (Jeppesen *et al.* 1998a), benefited from the refuge provided by macrophytes, especially thick floating flocks of *Lemna trisulca*, against 5-10 cm perch (III). The refuge effect was also indicated by the slightly increasing body size of euplanktonic cladocerans with macrophyte biomass towards the end of the experiment in the fish treatments (Fig. 8).

In the larger pan-European dataset, the variability of zooplankton responses to fish manipulations was influenced by substantial variation in community structure and macrophytic refuges among sites. For instance, the refuge effect for large crustacean grazers by the abundant *Myriophyllum* spp. was evident in Leon (IV, Fernández-Aláez *et al.* 2004). *Chara* beds have also been considered as good refuges for zooplankton against fish predation (Diehl 1988, Jeppesen *et al.* 1998a). However, *Chara* spp. at the study sites in Valencia and The Netherlands did not prevent efficient foraging of fish on large crustacean grazers (IV) (Van de Bund & Van Donk 2004, Romo *et al.* 2004). Even the lowest densities of fish (1.9-2.5 ind. m⁻²) used in the experiments of this thesis were near the threshold

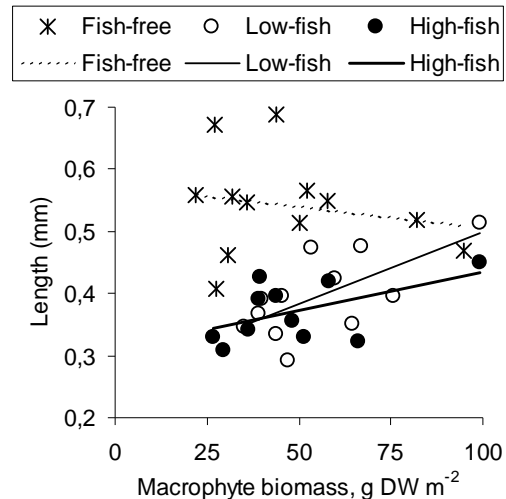


Figure 8. Relationships between the density-weighted mean length of euplanktonic filter-feeding cladocerans and the total biomass of macrophytes at the end of the experiment in 1999 in the different fish treatments (n = 12, except in high-fish treatments n = 11).

density (2-5 ind. m⁻²), at which the refuge effect of macrophytes may be partially or totally lost for cladocerans (Jeppesen *et al.* 1998a). However, such threshold fish density is probably shaped by the fish species and size/age-class, making generalisations difficult.

In contrast, plant-associated cladocerans benefited of macrophytic refuge against fish predation macrophytes. The biomass and body size of *Sida crystallina* O. F. Müller and several species of chydorids increased in *Elodea* beds and were even more abundant and larger in the presence than in the absence of 16-cm roach (I). *Lemna trisulca* also appeared to provide refuge for plant-associated cladocerans (chydorids and *Simocephalus vetulus* O.F. Müller) against 5-10-cm perch predation (III), indicated by the positive correlation between the final macrophyte biomass and cladoceran body size (Pearson; $r = 0.53$, $P = 0.009$; unpublished data). In addition to plant-associated cladocerans, the biomass of epiphytic

macroinvertebrates increased in *Elodea* beds (I; Fig. 2). Thus, within macrophyte beds, a shift from the dominance of planktonic communities towards that of plant-associated communities can be expected, with important consequences for competitive interactions of different fish species through food availability (Diehl 1993, Kornijów & Kairesalo 1994).

Alternative food sources for fish in the littoral habitat and consequences for fish-zooplankton interaction

According to the general view, roach are not only selective but also generalists shifting to the prey category that is most rewarding as a result of both the properties of an individual prey species and the density of the prey population (Townsend *et al.* 1986, Gliwicz 2002). In the enclosure experiment in Lake Vesijärvi, however, with the decreasing availability of cladoceran food roach switched to feeding on mainly detritus and plant material (I; Fig. 2) instead of using macroinvertebrates as an alternative food source as has been shown in laboratory studies (Horppila & Kairesalo 1992). Roach had a high search image for cladocerans and preferred them even when these became smaller and scarcer. In addition, roach had no influence on the biomasses of even the most eaten trichopteran and ephemeropteran larvae. Thus, the overall foraging of roach for macroinvertebrates was low and the unavailability of their preferred cladoceran food induced roach to increase consumption of less nutritious detritus/plant food. This result is in agreement with observations by Persson and Greenberg (1990). The capability for using alternative, less-preferred food sources may serve as life-supporting means for roach populations to manage

over periods of low cladoceran abundance. Thus, they are stabilised by the alternative food resources in littoral habitats and can maintain high predation pressure on zooplankton (cf. Schindler & Scheuerell 2002, Vadeboncoeur *et al.* 2002, Jeppesen *et al.* 2003). Among the many factors affecting predator-prey dynamics, the high preference for cladocerans is not likely to be a stabilising effect (Murdoch & Bence 1987, cf. Schindler & Scheurell 2002). On the other hand, in perch-dominated systems, macroinvertebrates may play a more important role as alternative prey knowing that perch are generally superior to roach in foraging for macroinvertebrates in vegetation (Persson 1987, Diehl 1988). For instance, in the experiment conducted in 1999 (Table 2), epiphytic animals such as chironomid and ephemeropteran larvae were relatively abundant within macrophyte beds (ca. 2-8 g m⁻²; unpublished data). They were efficiently preyed by the juvenile perch,

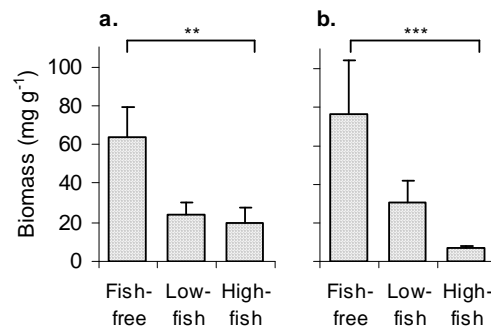


Figure 9. Mean (± 1 SE) biomass of epiphytic macroinvertebrates (DW per DW macrophytic biomass), excluding gastropods, in the different fish treatments on (a.) 7 July, 1999 and (b.) 4 August, 1999. Nutrient enrichment did not affect the macroinvertebrate biomass (ANOVA; $P > 0.05$). The results from the nutrient treatments were combined and, thus, each bar represents the mean of 12 replicates. Significant differences between the fish treatments (ANOVA; $P < 0.05$) are shown by the results of the Tukey's test in the figure (** $P < 0.01$, *** $P < 0.001$).

evidenced by their decreasing biomasses with fish (Fig. 9; unpublished data), which apparently contributed to the refuge effect observed for cladocerans against fish predation (III) (cf. previous chapter). These results emphasise the important role of submerged vegetation in modifying the foraging behaviour of different fish species and, consequently, affecting the predation pressure on zooplankton.

Diel vertical migration of littoral zooplankton in response to fish predation

Littoral zooplankton may undergo DVM between the lake bottom and open water in response to fish predation (Walls *et al.* 1990, Jeppesen *et al.* 2002b). Consequently, in mesocosms with 5-10-cm roach, higher biomasses of euplanktonic cladocerans (*Bosmina*, *Ceriodaphnia* and *Diaphanosoma*) were observed at night than during day (Fig. 10). However, the number of individuals was low and the variation between replicates high. The dominating

cladoceran, predaceous *Polyphemus pediculus* L. (cf. III), exhibited a similar behavioural pattern in the low-fish treatments (4 g FW m⁻²), while a contrasting trend was observed in the fish-free treatments (Fig. 10). *P. pediculus* typically occurs in dense swarms in the littoral zone and is considered a day-active animal migrating to the bottom during night (Butorina 1986). Apparently, the risk of fish predation can modify such behaviour. In the high-fish treatments (20 g FW m⁻²), the numbers of *Polyphemus* were reduced to low levels, unlike in the earlier experiment, where they were even positively affected by the presence of 16-cm roach (I). The discrepancy obtained here may reflect changes in the feeding preferences of roach with size. Despite their large body size, *P. pediculus* is not consistently preferred by roach due to their active escape reaction (Moss *et al.* 1998).

Thus, even in shallow waters plankton abundance may change due to DVM, especially when exposed to fish predation, and this should be taken into account when planning experiments. In

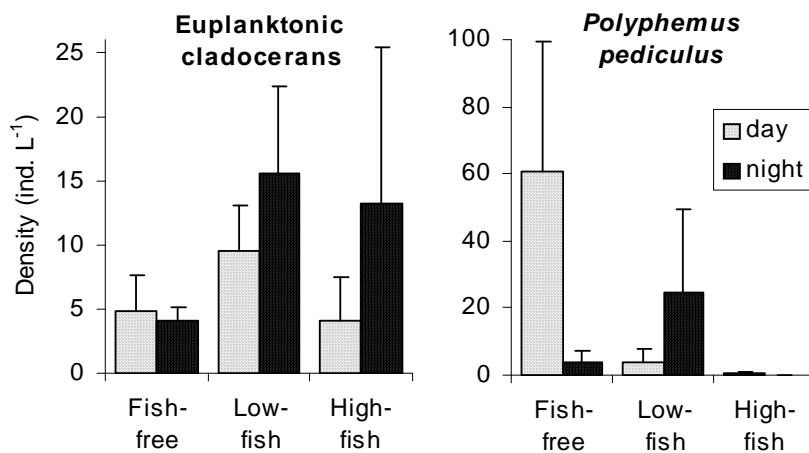


Figure 10. Mean (+ 1 SE) density of euplanktonic cladocerans and *Polyphemus pediculus* in the different fish treatments during day and night three weeks after the beginning of the experiment in 1998. Each bar represents the mean of 6 replicates, i.e. the results from both nutrient treatments were combined.

general, however, zooplankton may benefit less from DVM in response to fish predation in shallow than in deeper, stratified lakes (Sarvala *et al.* 1998). This is likely due to light penetrating down to the lake bottom, making vertical migration less advantageous (Burks *et al.* 2002).

Major effects of fish relative to nutrients in structuring the zooplankton community

The pan-European mesocosm experiment revealed remarkable year-to-year and geographical differences in zooplankton community structure and biomass (IV). This was partly attributed to differing weather conditions in northern and central Europe between the study years: summer 1998 was cool and windy, whereas summer 1999 was warm (IV; Table 1). However, some consistent patterns were evident. Fish had greater influence than nutrients in regulating zooplankton biomass, especially the relative abundances of different functional groups of zooplankton. The biomass of large crustacean grazers (> 0.5 mm) declined with the presence of fish (IV; Figs. 1 and 2, Table 2), thus addressing their sensitivity to predator manipulations, which is not a novel conclusion (Hrbáček *et al.* 1961, Brooks & Dodson 1965, Brett & Goldman 1997, Mehner *et al.* 2002, Shurin *et al.* 2002). At many sites, the biomass of predatory (raptorial) zooplankton, predominantly cyclopoid copepods, was also reduced by fish (IV; Figs. 2 and 3).

However, the responses of total zooplankton biomass to nutrient enrichment were mainly positive (IV; Figs. 1 and 3). For instance, in 1998 nutrient enrichment increased the biomasses of small crustaceans (< 0.5 mm) largely independently on the presence or absence of fish (IV; Table 2, Fig. 3). Macrophytes appeared to weaken

the effects of fish in some of the experiments. Small zooplankton species apparently benefited from the mostly negative responses of their predators and larger competitors to the presence of fish. Such compensation suggests a ratio-dependent functional response and is consistent with the view that nutrient enrichment leads to proportional increases at all trophic levels (Arditi & Ginzburg 1989, Leibold *et al.* 1997). It also emphasises the importance of compositional changes within trophic levels and reveals the limitation of simple food chain and ratio-dependent models in capturing such changes, as pointed out by Leibold *et al.* (1997), Hulot *et al.* (2000) and Persson *et al.* (2001).

4.2 Stability of littoral ecosystems and the control of phytoplankton biomass within macrophyte beds

Confounding effects of macrophytes on phytoplankton

Zooplankton grazing in vegetation plays a central role in controlling phytoplankton (Schriver *et al.* 1995, Jeppesen *et al.* 1998a, 1999). However, Meijer *et al.* (1999) and Blindow *et al.* (2000) suggested that more direct interactions between macrophytes and planktonic algae, rather than mere grazing of algae by zooplankton, are probably the decisive factors in controlling algal densities in lakes with dense submerged vegetation. Submerged macrophytes are regarded as P and N sinks during their active growth, thus suppressing the growth of phytoplankton, especially cyanobacteria (reviewed in Søndergaard & Moss 1998). In addition, P retention increases within rooted macrophyte beds such as *Elodea canadensis* through root oxygen release suitable for the formation of complexes of P with iron (Fe) (Hupfer & Dollan 2003). However, several studies showed that macrophytes do not

necessarily affect nutrient availability for phytoplankton and that nutrient competition between macrophytes and phytoplankton may be relatively unimportant (Schriver *et al.* 1995, Beklioglu & Moss 1996, Van Donk & Van de Bund 2002). In agreement with these observations, the results of this thesis suggested that macrophytes and their associated periphytic communities did not appreciably affect nutrient concentrations in the water and were unlikely to have caused nutrient limitation of phytoplankton (I; Table 1) (II; Fig. 1, Appendix A) (III; Fig. 3).

Macrophytes may have negative effects on phytoplankton through shading, but phytoplankton can overcome the problem of light limitation through buoyancy and motility (Søndergaard & Moss 1998). The abundant floating flocks of *Lemna trisulca* reduced photon flux density by 90-95% immediately below the flocks but only 0-40% at the bottom due to scattering of light (III). The surface coverage as well as the final biomass of *Lemna* correlated weakly with chl *a* concentration (Fig. 11), suggesting minor effects on phytoplankton through shading. Moreover, the phytoplankton was dominated by mobile, flagellated algae such as *Chlamydomonas* and *Volvox* (III).

The dense beds of *Elodea canadensis* also showed consistently low chl *a* concentrations (I; Fig. 1) and cyanobacterial biomasses (Fig. 12), even when the zooplankton biomass was relatively low, suggesting that phytoplankton production was directly or indirectly constrained by *Elodea*. Even though fish had a negligible effect on the total biomass and clearance rate of euplanktonic grazers, approximately 2-fold higher phytoplankton biomasses with slightly more edible algae such as cryptophytes and chlorococcales were observed in all *Elodea* treatments with roach as compared to the corresponding

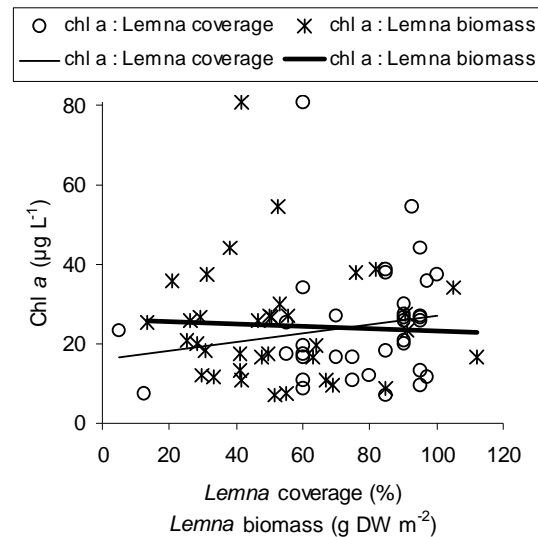


Figure 11. Relationships between the time-weighted average chl *a* concentration and the coverage and biomass of *Lemna trisulca* (Pearson; $P > 0.05$) ($n = 36$).

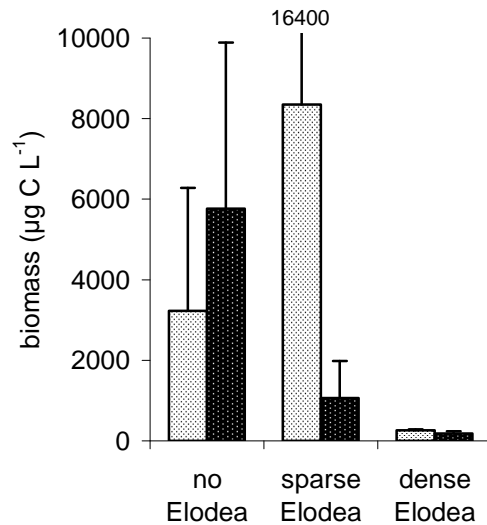


Figure 12. Mean (+ 1 SE) biomass of cyanobacteria in the different *Elodea* enclosures with or without fish during the middle of the experiment on 14 August, 1994.

fish-free enclosures (I). Thus, fish had a positive cascading effect on phytoplankton biomass via zooplankton grazers that addressed the role of grazing in controlling phytoplankton within macrophyte beds. Even though no differences in dissolved nutrient concentrations between the treatments

could be measured, this cascade was also evident via nutrient regeneration by fish (I). Enhancement of P and/or phytoplankton with fish was attributed to P inputs by fish in several previous experiments (e.g. Horppila & Kairesalo 1992, Järvinen & Salonen 1998, Vanni 2002), also emphasising the role of resource control relative to predator control.

Littoral ecosystem resistance and resilience to phosphorus enrichment

Littoral planktonic communities readily responded to both pulse and press P enrichments, although the major sink for the added P was well oxygenated surface layers of the sediment (II). However, periphytic chl *a* concentration and accumulation of P by periphyton were low even with press P enrichment (II; Table 1, Appendix B), thus contrasting earlier observations of the major role of periphytic communities in the nutrient dynamics of littoral areas (cf. Wetzel and Søndergaard 1998).

Planktonic responses to P enrichment differed between *Elodea* treatments and no-*Elodea* treatments. P enrichment resulted in higher biomasses of cyanobacteria (*Anabaena circinalis* Rabenhorst and *A. spiroides* Klebahn), greater concentrations of microcystins and lower biomass of cladocerans (predominantly *Daphnia longispina* and *Sida crystallina*) in the absence, as opposed to the presence, of *Elodea* (II; Figs. 2, 3). Thus, measured as cyanobacterial biomass, no-*Elodea* treatments had a lower resistance to press and pulse P enrichments than *Elodea* treatments (II; Fig. 4). Both *Elodea* treatments were also resilient, returning to reference conditions after pulse P

enrichment, except for one no-*Elodea* enclosure, which had a low biomass of filter-feeding cladocerans and in which high cyanobacterial biomasses developed even after pulse P enrichment. The calculated return time was slightly lower in *Elodea* treatments (16 ± 7 (SE) days, $n = 3$) than in no-*Elodea* treatments (21 ± 4 days, $n = 2$).

Grazing by large cladocerans, which increased towards the end of the experiment, probably contributed to the recovery of the littoral ecosystem. Evidently, however, *Elodea* was able to regulate the growth of *Anabaena* directly or indirectly (I, II), thus strengthening the resistance and resilience of the system against P enrichment (II). Organic compounds released by macrophytes may inhibit the growth of cyanobacteria (cf. Gross 2003) and stimulate bacterial production, increasing thereby the uptake of P by bacteria at the expense of phytoplankton (Søndergaard & Moss 1998, Søndergaard *et al.* 1998, cf. Järvinen & Salonen 1998). This indirect, plant mediated P pathway may also have contributed to the suppression of *Anabaena* through feeding on P-rich bacteria by cladocerans, especially by *D. longispina* (cf. Kankaala 1988, Salonen *et al.* 1994, Jeppesen *et al.* 1996, Järvinen & Salonen 1998). *Daphnia* and several other cladocerans also recycle nutrients with high N:P ratios and may thus reduce the competitive success of cyanobacteria with low optimal N:P ratios (MacCay & Elser 1998). Moreover, they release nutrients in organic rather than in inorganic forms, thus supporting heterotrophic rather than autotrophic processes in ecosystems (Anderson *et al.* 2005). The results of the enclosure experiment in 1996 showed that submerged plants regulate phytoplankton-zooplankton interactions in lake littoral (II).

Macrophytes lowered the total toxin production of cyanobacteria but did not affect the specific toxicity. Toxin-producing strains of cyanobacteria are favored by high concentrations of P (Rapala *et al.* 1997) and by direct or indirect exposure to zooplankton (Jang *et al.* 2003). In this experiment, however, P enrichment did not evidently increase the mass-specific toxicity and no correlation was found between toxicity of cyanobacteria and zooplankton biomass. This, in fact, was to be expected since zooplankton biomasses and species composition did not differ drastically between the treatments. This result also suggests tolerance against toxic cyanobacteria in *Daphnia* and other zooplankton, in accordance with observations by Gustafsson and Hansson (2004).

Littoral ecosystem resistance to phosphorus and nitrogen enrichment

The central role of the littoral community structure in determining the resistance to nutrient enrichment with both N and P was demonstrated also in two consecutive years (1998 and 1999) with contrasting abundance of macrophytes and cladocerans (III). When macrophytic growth was poor, filter-feeding cladocerans were scarce (initial biomass < 10 $\mu\text{g C l}^{-1}$) and the zooplankton community was dominated by cyclopoid copepods and rotifers, enrichment provoked a turbid water state with high planktonic (predominantly chlorophytes and cryptophytes) and periphytic algal biomasses, masking the effects of fish on algal biomasses (III; Table 2, Figs. 1, 2). Under the low-temperature conditions prevailing in early summer, the start of macrophyte growth was delayed, and further suppressed by the development of planktonic and periphytic algal biomasses in the enriched mesocosms. A clear-water state with low

phytoplankton biomass occurred only in unenriched mesocosms without fish or with low fish biomass (4 g FW m^{-2}). Roach further increased turbidity inside the mesocosms, as evidenced by the higher amounts of total suspended solids (ANOVA; $F_{2,8} = 5.70$, $P = 0.046$; Fig. 13; unpublished results), while the clearance rate of cladocerans was equally low in all fish treatments (III; Fig. 2). Even though weather conditions were cool and windy, turbidity was low in the open lake area

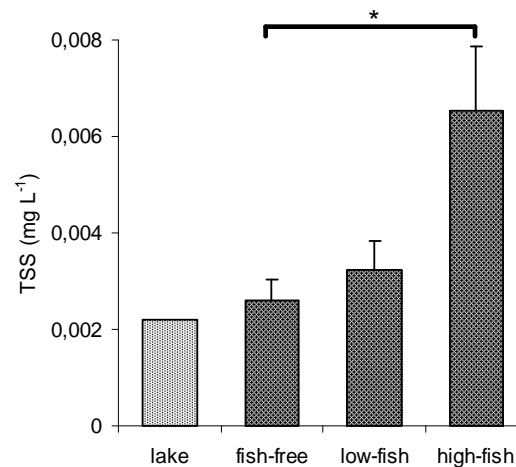


Figure 13. Mean (± 1 SE) values of time-weighted averages of total suspended solid (TSS) concentrations in the different fish treatments ($n = 3$) as well as in the nearby lake area outside the enclosures. Only nonenriched treatments are included in the figure. The asterisk shows the result of the Tukey's test.

outside the enclosures (Fig. 13). Thus, fish-induced resuspension is an important factor causing turbidity in lake littoral zones, in accordance with several previous studies (Horppila & Kairesalo 1992, Horppila 1994, Horppila & Nurminen 2003).

When macrophytes (mainly *Lemna trisulca*) were abundant and the zooplankton community was dominated by filter-feeding cladocerans (*Diaphanosoma* and *Ceriodaphnia*; initial biomass > 100 $\mu\text{g C l}^{-1}$) (III; Fig. 2), a clear-water state with low phytoplankton biomass prevailed even under the highest

levels of nutrient enrichment (III; Fig. 1). The cladoceran grazing rate increased with nutrients and controlled the phytoplankton biomass, but the cascading effect of fish shown by the reduced grazing rate and increased chl *a* concentration became evident between the low- and high-fish treatments (Tukey; $P = 0.001$ and $P = 0.039$, respectively) (III; Fig. 1). Only fish but not nutrients affected the phytoplankton biomass (III; Table 5); however, at the two highest nutrient levels the threshold fish biomass was even above 20 g FW m⁻² also suggesting a high growth rate of cladocerans with nutrients. *Ceriodaphnia* are small (< 0.7 mm in this experiment) but they can have high mass-specific grazing rates (Mourelatos & Lacroix 1990). They, as well as *Diaphanosoma*, are efficient microfiltrators of bacterioplankton (DeMott 1986) and thus well adapted to macrophyte beds (Jeppesen *et al.* 1998a). Similar plant-mediated nutrient pathways via bacteria and heterotrophic processes, as suggested by observations with *Elodea* (II) in the previous chapter, probably also operated in systems with abundant *Lemna*. In addition, the capability of *Ceriodaphnia* for incorporating high amounts of P relative to N is comparable to that of *Daphnia* (Hessen & Lyche 1991). Thus, nutrient cycling by cladocerans may also have controlled phytoplankton growth.

Thus, ecosystem resistance may be high and the sensitivity of phytoplankton biomass to nutrient input low with abundant, relatively small cladocerans in accordance with the observations by e.g. Helminen and Sarvala (1997) and Cottingham *et al.* (2004). However, more pronounced effects of zooplankton on phytoplankton are often seen with large *Daphnia* as the key grazer (cf. Carpenter *et al.* 1985, Carpenter & Kitchell 1993, Mazumder 1994, Cyr & Curtis 1999). Furthermore, analyses of major species, not only keystone species, with careful considerations about their interactions

within the community may provide insights into ecosystem functioning (cf. Hulot *et al.* 2000), an important aspect especially in littoral ecosystems.

Role of plant-associated animals in controlling phytoplankton and periphyton

Plant-associated cladocerans, less vulnerable to fish predation than euplanktonic species (I, III) (Chapter 4.1), can have high grazing impact on phytoplankton (Jeppesen *et al.* 1998a, Balayla & Moss 2004). *Sida* is an especially efficient filter feeder (Balayla & Moss 2004), while chydorids scrape on periphyton and are considered less effective grazers (Lövgren & Persson 2002). The biomasses of these cladocerans increased with macrophytes and were likely even higher than observed, since water sampling underestimated the numbers of plant-associated species (I-III). *Elodea* also sustained rich assemblages of herbivorous and detritivorous macroinvertebrates (I). Thus, *Elodea* harboured herbivores capable of controlling not only phytoplankton but also periphyton, which are qualitatively different forms of primary producers. Grazing was considered as a possible explanation for the slight accumulation of periphytic biomass on plastic strips despite P enrichment (II). This addresses the importance of taking into consideration the trophic level heterogeneity in littoral ecosystems (cf. Lövgren & Persson 2002). The complexity of littoral habitats involving different forms of primary producers also addresses the limited capability of the food chain theory for considering such heterogeneity. Separating the two communities is also difficult since they are linked via predators and behavioural patterns. For instance, several plant-associated

cladocerans such as *Sida* also swim freely at night (Walls *et al.* 1990).

Control of phytoplankton biomass by zooplankton grazers: geographical differences

Increase in the biomass of rotifers was generally associated with an increase in chl *a*, indicating the low ability of these specialised suspension feeders to control total phytoplankton biomass (IV; Table 3). On the other hand, through providing food for fish larvae, rotifers may maintain a high recruitment of zooplanktivorous fish and therefore the role of rotifers is emphasised under turbid conditions. At many sites, the biomass of small crustaceans also had a positive or insignificant correlation with chl *a* (IV; Table 3). In contrast, the biomasses of large crustacean grazers were inversely related to the chl *a* concentrations, except at the highest temperature (close to 30 °C) in Valencia where chl *a* was unrelated to the biomass of large crustacean grazers (IV; Table 3) and the overall biomass of large cladocerans was low compared with that at other study sites (IV; Fig. 2). This result suggests that the role of grazing in controlling phytoplankton biomass by especially large grazers was important at all sites except in Valencia. The dataset, however, was insufficient to show whether there could be a threshold between temperature regimes at which the functioning of ecosystems would markedly change (cf. Scheffer & Carpenter 2003). Increase in the biomass of small grazers and rotifers was generally associated with an increase in chl *a* (IV; Table 3), indicating the low ability of small zooplankton to control total phytoplankton biomass.

At the high temperatures in Valencia, nutrient enrichment apparently led to inharmoniously more rapid growth rates of algae compared with those of

zooplankton and thus disrupted top-down control of algae (cf. Arditi & Ginzburg 1989, Power 1992). In addition, the crustacean zooplankton biomass was efficiently reduced by fish, supporting the statement that with increasing temperature the herbivore control will further weaken with respect to resource control if the disruption of trophic regulation is interfered with predators (Power 1992). Apart from the reduced role of large crustacean grazers in the southernmost location in Valencia, no consistent geographical patterns were observed in the responses of zooplankton communities to nutrient and fish manipulation. Other potential geographical differences were probably masked by the high year-to-year variation in prevailing weather conditions. Such environmental variability may greatly affect the structure and functioning of littoral communities (cf. III).

*Role of zooplankton grazing in explaining the variation between chlorophyll *a* and total phosphorus*

A steep slope between chl *a* and total phosphorus (TP) concentration suggests a cascading effect of fish through herbivorous zooplankton on phytoplankton in systems with three trophic levels (Hansson 1992) and can be found in non-stratified lakes lacking large zooplankton grazers (Mazumder 1994, Sarvala *et al.* 1998). The results from the high-fish treatments (20 g FW m⁻²) of the pan-European experiment agree with these predictions and were evidenced by the generally low biomass of large grazers and consistently high biomass of phytoplankton with increasing nutrients (IV; Fig. 4e). However, the slope in the low-fish treatments was less steep and similar to that in the fish-free treatments. Perhaps small crustacean grazers and plant-associated cladocerans that benefited from the macrophytic refuge

and were not heavily preyed upon by fish probably played at least a complementary role in controlling phytoplankton biomass, as was shown in the Finnish mesocosm experiment in 1999 (III) (Chapter 4.2, pages 25-26). Thus, zooplankton controlled phytoplankton when fish were not abundant (≤ 4 g FW m^{-2} or 2.5-4 ind. m^{-2}). Cladoceran body length is an important predictor of phytoplankton biomass and water clarity (Carpenter *et al.* 1998, Stemberger & Miller 2003) and was suggested also by

observations in Lake Vesijärvi (Chapter 1.5). On the other hand, in some systems, e.g. in shallow, non-stratified Lake Pyhäjärvi with planktivorous fish biomass of < 30 kg ha^{-2} (i.e. 3 g m^{-2}), total cladoceran biomass consisting of relatively small individuals explained much of the variation in chl *a* concentration (Sarvala *et al.* 1998).

Despite the scarcity of the keystone grazer *Daphnia*, the total abundance of large crustacean grazers (predominantly *Diaphanosoma*, *Sida*, *Simocephalus*,

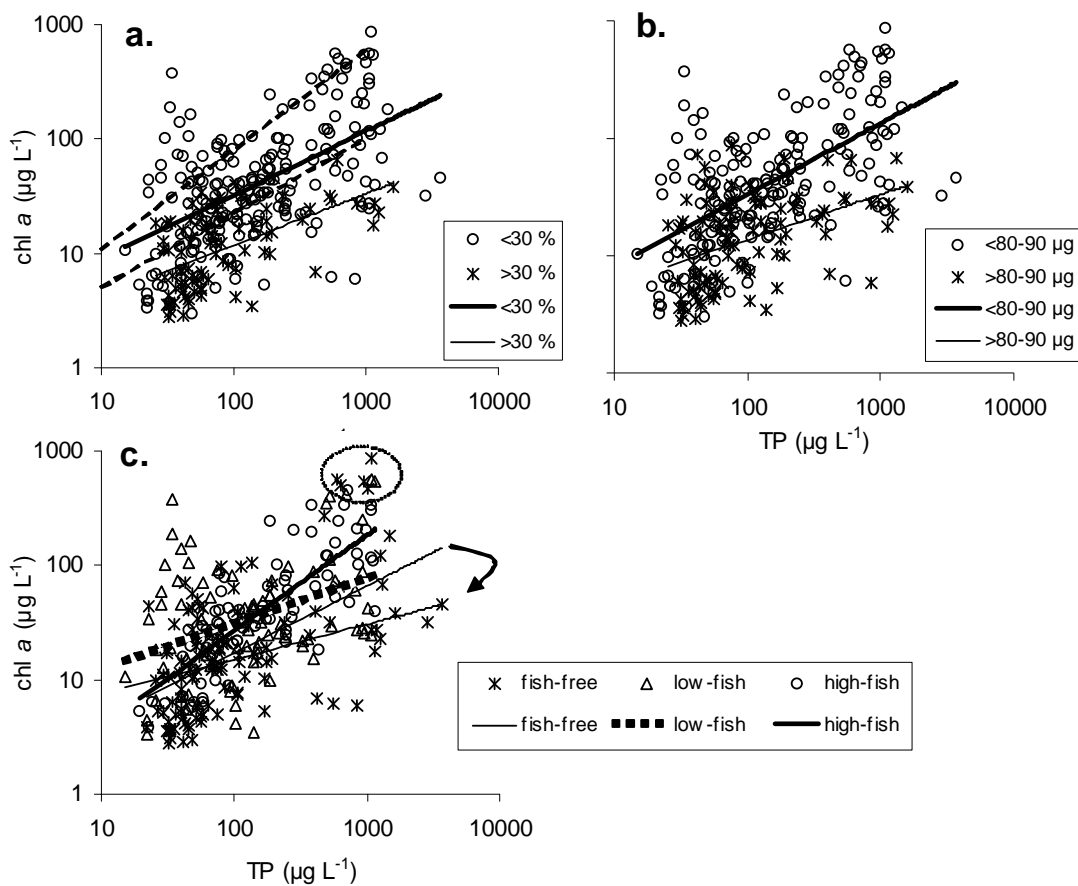


Figure 14. Relationship between concentrations of chlorophyll *a* (chl *a*) and total phosphorus (TP) in enclosures and mesocosms with a biomass of large grazers below and above (a.) 30% and (b.) 80-90 $\mu\text{g DW l}^{-1}$ of the total zooplankton biomass as well as with (c.) three fish densities. Data are from experiments carried out in Lake Vesijärvi in 1994, 1996, 1998 and 1999 and at five other shallow lake sites across Europe in 1998 and 1999. Note the logarithmic presentation of both axes. Panel a. also shows the regressions from Mazumder (1994) for northern temperate non-stratified lake ecosystems having (lower dashed line) or lacking (upper dashed line) large *Daphnia*. The circle in panel c. shows the data points from fish-free, high-nutrient treatments in Valencia with negligible biomass of large grazers. The arrow shows how the slope of the fish-free regression line changes when excluding these data points (see text for further explanation).

Eudiaptomus) explained the relationship between chl *a* and TP better than did the mere number of trophic levels. When abundant ($> 80\text{-}90 \mu\text{g DW l}^{-1}$; IV), large grazers controlled phytoplankton biomass even under hypertrophic conditions (up to $1600 \mu\text{g TP L}^{-1}$). Otherwise, the chl *a* concentration increased steeply with increasing TP concentration (IV; Fig. 4d). This threshold biomass is close to that ($100 \mu\text{g DW l}^{-1}$) observed by Hansson (1992). However, even stronger differences in the TP:chl *a* ratio were found in systems with sparse/abundant *Daphnia* (Sarnelle 1992). In reality, however, hypertrophic conditions with low biomass of fish and high biomass of large zooplankton are rare except after fish kills or in effectively biomanipulated lakes with abundant submerged vegetation (cf. Sarvala *et al.* 1998, 2000).

Phytoplankton control by grazing has been shown to be consistently low, when *Daphnia* constitutes $< 20\%$ of zooplankton biomass, while above this threshold grazing potential is high (Brooks & Dodson 1965, Mazumder 1994). The empirically observed threshold proportion of large grazers in the pan-European data set was similar in magnitude (ca. 30%) although not directly comparable, due to the lack of large *Daphnia* in most systems. The ratios between the concentrations of TP and chl *a* may be sensitive to further data points. However, when the dataset was supplemented with the results obtained in the experiments conducted in 1994 and 1996 in Kilpiäistenpohja Bay (I, II) (Table 2), the TP:chl *a* ratios remained essentially similar (Fig. 14a, b). Both grazer systems had smaller slopes than those obtained by Mazumder (1994) from several northern temperate non-stratified lake ecosystems and enclosure experiments under contrasting grazer communities (Fig. 14 a). This may reflect also other mechanisms besides grazing in the control of phytoplankton in shallow littoral ecosystems such as those related

to macrophytic regulation of phytoplankton growth. The low resistance of the systems in the southernmost location in Valencia to nutrient enrichment even in the absence of fish can be discerned as a separate group of data points (denoted by a circle in Fig. 14c). When excluding these data points, the slope became even less steep (denoted by an arrow in Fig. 14c).

On the other hand, the phytoplankton biomass was positively related to the TP concentration even in the presence of efficient grazers, thus reflecting the positive response of adjacent trophic levels, inconsistently with traditional foodchain theory. This observation is in agreement with the results of several earlier studies from mesocosm to whole-lake scale (Hansson 1992, Mazumder 1994, Brett & Goldman 1997, Leibold *et al.* 1997, Hansson *et al.* 1998c, Sarvala *et al.* 1998, Persson *et al.* 2001). Ultimately, ecosystem productivity is quantitatively more important than consumer regulation in determining the biomass of primary producers. Nevertheless, the results of this thesis showed that zooplankton grazers play an important role in controlling phytoplankton, in accordance with several earlier studies (e.g. Carpenter *et al.* 1985, 1993, Hansson 1992, Sarnelle 1992, Sarvala *et al.* 1998, 2000, Cyr & Curtis 1999, Jeppesen *et al.* 1999, 2003, Persson *et al.* 2001). Community structure, especially the abundance of zooplankton grazers together with macrophytes, is of crucial importance in determining the stability of the littoral ecosystem as well as its resistance to nutrient loading. Thus, food web management can be a useful tool for affecting water quality of northern and temperate eutrophic lakes.

4.3. Field mesocosm experiments and their applicability for studying aquatic ecosystem functioning

Experimental mesocosm systems may produce results quite comparable with natural systems (Sarnelle 1992, Mazumder 1994). Nevertheless, they involve the problem of both spatial and temporal scale that exclude some of the ecosystem processes and tend to increase the strength of food web interactions and the trophic cascade (Schindler 1990, Carpenter & Kitchell 1993). This phenomenon was also revealed by several results of the experiments in this thesis and has been discussed in the text. It also addresses the cautiousness called for in interpreting their results and generalising them across larger scales.

Littoral community structures, especially the abundance of macrophytes and efficient zooplankton grazers, appear to be driven largely by prevailing weather conditions (III, IV, Stephen *et al.* 2004). Long-term variation in lake food web structure and water quality is dependent on climatic fluctuations, strongly determined by spring and summer wind and temperature conditions, that affect the variation in fish year-classes as well as the establishment of submerged vegetation and thus indirectly zooplankton and phytoplankton development (cf. Sarvala *et al.* 1998, Hargeby *et al.* 2004). Thus, multiple stresses from climatic and biotic variables modify patterns within a lake ecosystem in different years (III, IV) (cf. Salonen *et al.* 1990, Hargeby *et al.* 2004). Small-scale experiments can be helpful in explaining the mechanisms behind such larger-scale patterns as well as ecosystem responses to perturbations in more detail (Scheffer & Carpenter 2003). For instance, complex direct and indirect ways, through which submerged macrophytes affect littoral nutrient and plankton dynamics (II) would probably be impossible to document without

controlled experiments. In addition, studying the responses of littoral ecosystems to perturbation is complicated by the patchy, heterogeneous nature of these habitats. Such practical constraints determine the experimental design.

Differences in the starting conditions, i.e. community structure, are crucial to the outcome of perturbations such as nutrient enrichment (II, III, Stephen *et al.* 2004). Even in the absence of environmental heterogeneity, the initial state and variation in community assemblages across landscapes of community patches can result in variable outcomes (Drake *et al.* 1996). Such observations emphasise the limitations and reproducibility of field experimentation (Polis and Winemiller 1996, Moss *et al.* 2004). High deviation of several results obtained in the experiments of this thesis also addresses the need to have preferably more than two or three replicates of each treatment. On the other hand, the basic understanding of how ecosystems respond to perturbations is increased by the knowledge about how different initial conditions may lead to different final states. Field experiments can be a powerful way to show alternative attractors of systems (II, III) (Scheffer & Carpenter 2003). This, in turn, has practical implications for the management and restoration of lake ecosystems in order to increase their resistance and resilience to anthropogenic perturbations.

5. CONCLUSIONS AND FUTURE RESEARCH NEEDS

Initial community composition, primarily the abundance of submerged macrophytes and cladoceran grazers, played the decisive role in determining the stability of littoral ecosystems and resistance to nutrient enrichment, recorded as lower biomass of phytoplankton. When the abundance of macrophytes and cladocerans was low, P enrichment favoured cyanobacteria, while P and N enrichment favoured chlorophytes and cryptophytes as well as periphytic algae. Wide year-to-year variation in littoral community composition was determined largely by prevailing weather conditions. Such variable conditions may cause oscillations in the habitat coupling between littoral and pelagial zones, for instance, through variable recruitment and foraging behaviour of fish.

A submerged macrophyte *Elodea canadensis* hampered the growth and toxin production of cyanobacteria and regulated phytoplankton-zooplankton interactions, although littoral ecosystems even without macrophytes could be resilient and recover from instantaneous P loading when cladoceran grazers were abundant. The mechanisms underlying the control of cyanobacterial growth by macrophytes proved to be complex and apparently involved direct and indirect effects through allelopathy as well as altered nutrient cycling which was also influenced by heterotrophic processes of the microbial compartment. More detailed experiments and techniques are needed to reveal such processes and their relative role in controlling phytoplankton growth in field conditions.

The results emphasised the general importance of consumer control over resource control in determining zooplankton community structure in shallow lake systems. The results are in agreement with the general view that

(large) herbivores respond strongly to predator manipulations in aquatic food webs. However, different growth forms of submerged macrophytes were of variable value as refuges for zooplankton against fish predation. Especially plant-associated and small euplanktonic cladocerans benefited from macrophytic refuge and were able to control phytoplankton when fish predation pressure was not high ($\leq 2.5\text{-}4$ fish m^{-2} or ≤ 4 g FW m^{-2}). The results suggested that analyses of major cladoceran species, not only keystone species, with careful considerations about their interactions within the community may provide insights into littoral ecosystem functioning. The refuge value of different macrophytic species and growth forms in a fluctuating environment both in space and time varies, being a subject for further studies.

Roach preferred feeding on cladocerans even as they declined in abundance, but also used less-preferred, mainly non-animal food sources as alternative food. Switching of prey preference and, consequently, reduction in the predation pressure on cladocerans could not, however, be evidenced. Thus, littoral subsidies may maintain omnivorous and planktivorous fish populations such as roach under conditions with low cladoceran abundance and this support may intensify rather than dampen the strength of the interactions between fish and zooplankton. In a long term, on the other hand, fish assemblages and the fish-mediated coupling of pelagic and littoral processes change with macrophytic vegetation also affecting plankton dynamics. More evidence for such long-term patterns in littoral zones would be valuable to increase our understanding of ecosystem functioning and coupling between littoral and pelagial under fluctuating environmental conditions.

Geographical differences in the responses of zooplankton communities to

nutrient and fish manipulation were probably masked by wide year-to-year variation in the prevailing weather conditions. The only consistent geographical pattern was the reduced role of large crustacean grazers in the southernmost location in Valencia compared with the other sites. Thus, although food web management may be a useful measure in northern and temperate locations, nutrient control may be more important in southern lakes. This conclusion needs further research especially in warm weather conditions in order to predict how climate change should be taken into consideration when planning restoration measures for eutrophicated lakes.

The phytoplankton biomass was positively related to TP concentration even in the presence of efficient grazers. This result reflects the positive response of adjacent trophic levels and the ultimate, quantitatively important role of productivity compared with consumer

regulation in determining the primary producer biomass. However, the abundance of large crustacean grazers explained reasonably well the variance between productivity and algal biomass, even better than did the mere number of trophic levels. This may be explained by confounding factors such as heterogeneity within the habitat and trophic levels, often difficult to disentangle from each other.

In summation, the abundance of zooplankton grazers and macrophytes was of crucial importance in determining the stability of the littoral ecosystem evidenced as high resistance to nutrient loading. In northern temperate eutrophic lakes, this beneficial community structure may be achieved and maintained by controlling the planktivorous and omnivorous fish populations that are supported by both pelagic and littoral resources and may contribute to the trophic state throughout the lake.



6. ACKNOWLEDGEMENTS

Analogously to food web theory, belief in the accomplishment of this work has varied, exhibiting relatively discontinuous, alternating (high/low/high) changes with the increase in the amount of samples, Excel sheets, various statistical analyses and manuscript versions. Apart from constructing field experiments and interpreting their complicated results, the SIL congress, among other things, showed that practically nothing is impossible – not

even stepping across the threshold of making a thesis.

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