RESPONSE OF MACROINVERTEBRATES IN LAKES TO BIOMANIPULATION AND CLIMATE CHANGE

PhD Thesis
Thomas Boll

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NATIONAL ENVIRONMENTAL RESEARCH INSTITUTE
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Abstract: Effects of biomanipulation (i.e. removal of benthivorous and zooplanktivorous fish) on macroinvertebrates and their role in the recovering processes of shallow lakes were studied mainly in Danish Lake Væng. Density of benthic macroinvertebrates peaked two years after biomanipulation, coinciding with the establishment of submerged macrophytes and the reduced predation pressure from benthivorous bream and roach. During years with dense macrophytes $\delta^{13}C$ of invertebrates increased markedly, likely because the submerged macrophytes reduced the CO_2 concentration in the lake water and the flow of ^{13}C-depleted CO_2 from the sediment to the water phase, leading to higher $\delta^{13}C$ of phytoplankton and, consequently, of consumers. Analyses of $\delta^{13}C$ in remains of invertebrates in the sediment may therefore be a useful tool for identifying a shift from the clearwater macrophyte stage to the turbid phytoplankton stage in the past. Establishment of submerged macrophytes after biomanipulation can be delayed, but artificial plant beds may act as an alternative substrate and refuge for invertebrates in the initial recovery phase of lakes. During the second biomanipulation artificial plants positioned in the lake harboured high densities of macroinvertebrates. These may serve as prey for perch, allowing them to grow faster to the piscivores stage, where they can prey on cyprinids. However, lower densities of plant-associated macroinvertebrates found in subtropical lakes and a potential increase in fish densities in temperate lakes due to global warming indicate that we can expect a reduction in the abundance of plant-associated macroinvertebrates in a future warmer climate.

Keywords: Macroinvertebrates, biomanipulation, lake restoration, stable isotope analysis, perch, artificial plants, submerged macrophytes, climate change, global warming, temperate shallow lakes, bioturbation

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Content

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List of manuscripts

Manuscript 1

Boll, T., Johansson, L.S., Lauridsen, T.L., Landkildehus, F., Søndergaard, M., Andersen, F.Ø. & Jeppesen, E. Changes in benthic macroinvertebrate community and lake isotope (C, N) signals following biomanipulation: an 18-year study in shallow Lake Væng, Denmark. Manuscript.

Manuscript 2

Boll, T., Balayla, D., Andersen, F.Ø. & Jeppesen, E. Plant-associated macroinvertebrate response to biomanipulation: An experiment with artificial plant beds with contrasting densities. Manuscript.

Manuscript 3

Boll, T., Meerhoff, M., Clemente, J.M., Vianna M., Kröger A., Pedersen, A.R. & Jeppesen, E. Plant-associated macroinvertebrates in temperate and subtropical shallow lakes along trophic and fish predation gradients. Manuscript.

Manuscripts are not included in the electronic version of this thesis.

1 Summary

The existence of two alternative stable states in shallow temperate lakes, a clear and a turbid state, has led to the development of numerous lake restoration methods in an attempt to shift eutrophic lakes back to the clear water state with high abundance of submerged macrophytes. One of these methods is biomanipulation that has been successfully used for decades.

The aim of this thesis is to describe how biomanipulation (here a term for removal of benthivorous and zooplanktivorous fish) affects communities of macroinvertebrates and how macroinvertebrates potentially affect the recovering processes of the lake. The following four questions were sought answered. 1) How do reduced biomass of benthivorous and zooplanktivorous fish and expanding coverage of submerged macrophytes affect benthic macroinvertebrate communities? 2) How do benthic chironomids affect release of nutrients from the sediment in shallow lakes? 3) How are macroinvertebrate communities reacting to establishment of macrophyte beds and how do changes in fish community and environmental parameters following biomanipulation affect these plant-associated macroinvertebrates? 4) How do interactions between macroinvertebrates, plants and fish in lakes in warmer climates differ from those between macroinvertebrates, plants and fish in temperate lakes today? The last question is formulated so as to consider the potential impact of global warming on biomanipulation effects.

The focus is on Danish Lake Væng where biomanipulation was performed in 1986-1988 and again in 2007-2008. After the first biomanipulation the lake shifted to a clear water state dominated by *Elodea canadensis*. The lake remained clear until 1997, when submerged macrophytes abruptly disappeared, and the turbid state was re-established. From 2009, after the second biomanipulation, the lake returned to the clear state and was again with *E. canadensis* dominance.

The density of benthic macroinvertebrates was studied during the period 1988-2006 where large fluctuations in densities occurred. In 1990, two years after the biomanipulation, macroinvertebrate density peaked, mainly due to high numbers of chironomids. This density increase was most likely caused by reduced predation pressure from bream (*Abramis brama*) and roach (*Rutilus rutilus)* and increased coverage of submerged macrophytes. Overall, the density of macroinvertebrates was higher in years with submerged macrophytes than in years without macrophytes, which may partly be explained by the refuge against fish predation provided by the macrophytes, and partly by the higher number of plant-associated macroinvertebrates occurring in the samples in those years.

In 1990, the number of *Chironomus* larvae was about 1400 ind. m^{-2} higher than the average density for the entire period. Results from bioturbation experiments conducted with sediment from Lake Væng showed that such an increase in the density of *Chironomus* larvae may result in a significantly higher release of ammonium, soluble reactive phosphorus and total phosphorus from the sediment, and likely also higher denitrification.

Analyses of stable carbon and nitrogen isotopes were subsequently performed on the benthic macroinvertebrates (preserved with ethanol), on zooplankton (preserved with Lugol's solution) and on scales of roach.

Macroinvertebrates, cladocerans and cyclopoid copepods had higher $\delta^{13}C$ in years where submerged macrophytes were present in the lake. We hypothesise that dense stands of *E. canadensis* reduced CO_2 concentrations in the lake and the flow of ^{13}C-depleted CO_2 from the sediment to the water phase, leading to higher $\delta^{13}C$ in phytoplankton and consequently in consumers during years with macrophytes. Fish scales were available only from a limited number of years, but the isotopic signals indicated that roach foraged in littoral areas during years of high turbidity, while zooplankton and macroinvertebrates in the open water obviously contributed more to the diet in years with clear water.

During the second biomanipulation in Lake Væng we placed artificial plant beds in the lake and studied the density of plant-associated macroinvertebrates. The density of macroinvertebrates increased throughout the year in 2007, while densities were lower in September and October 2008 and in 2009. Predation or habitat-avoidance caused by young-of-the-year perch (YOY) (*Perca fluviatilis*) presumably caused the decline in densities of macroinvertebrates on the artificial plants in 2008 as well as in 2009 when YOY perch were larger and likely more efficient hunters due to the low turbidity. However, the artificial plants supported high densities of macroinvertebrates and may thus be a useful tool to provide perch with a larger food source (prey invertebrates) when the establishment of natural submerged vegetation is delayed after biomanipulation and nutrient loading reduction. Potentially, enhanced growth of perch may lead to higher recruitment to the piscivorous stage.

To estimate potential effects of global warming on the interactions between macroinvertebrates, plants and fish, we compared macroinvertebrate communities in Denmark and Uruguay collected from artificial free-floating and submerged plants placed in lakes covering a trophic gradient. The density of macroinvertebrates per gram plant was lowest in the Uruguayan lakes, most likely due to the high densities of small herbivorous and omnivorous fish there. Free-floating plants generally supported higher densities of macroinvertebrates per gram plant than submerged plants and this difference was most pronounced in clear water. An explanation may be that the refuge offered by free-floating plants against fish predation via their shadowing effect lose significance when Secchi depth is reduced.

In conclusion, the establishment of submerged macrophyte beds following a reduction in the biomass of zooplanktivorous and benthivorous fish will overall lead to higher densities of macroinvertebrates despite that strong cohorts of YOY perch may initially have a negative impact on the abundance of plant-associated macroinvertebrates. Artificial plants may thus be used as a useful tool in the initial phase after biomanipulation if submerged macrophytes development is delayed, since they may provide perch with high densities of prey invertebrates allowing them to grow faster to the piscivores stage. However, lower densities of plant-associated macroinvertebrates found in subtropical lakes and a potential increase in fish densities in temperate lakes due to global warming indicate a reduction in the abundance of plant-associated macroinvertebrates in a future warmer climate.

2 Dansk resumé

Eksistensen af to alternative stabile tilstande i lavvandede tempererede søer, en klarvandet og en uklar, har betydet, at der i dag anvendes en række forskellige metoder inden for sørestaurering med henblik på at bringe eutrofierede søer tilbage i en klarvandet tilstand domineret af undervandsplanter. Biomanipulation (opfiskning af bentivore og zooplanktivore fisk) er én af disse metoder, der med succes har været anvendt i årtier.

Målet med denne afhandling er at beskrive, hvordan biomanipulation påvirker søens makroinvertebratsamfund, samt hvordan makroinvertebraterne potentielt kan påvirke søens miljøtilstand i forbindelse med restaureringsprocessen. Mere specifikt blev følgende fire spørgsmål søgt besvaret: 1) Hvordan påvirker en reduktion i biomassen af bentivore og zooplanktivore fisk samt en øget dækning af undervandsplanter de bentiske makroinvertebratsamfund? 2) Hvordan påvirker chironomider næringsstoffrigivelsen fra sediment i lavvandede søer? 3) Hvordan reagerer makroinvertebratsamfund på etableringen af makrofyter og hvordan vil ændringer i fiskebestanden og miljøfaktorer efter biomanipulation påvirke disse plantetilknyttede makroinvertebrater? 4) Hvordan vil interaktionerne mellem makroinvertebrater, planter og fisk i et varmere klima adskille sig fra det, der observeres i søer i tempererede egne i dag? Det sidste spørgsmål er formuleret med henblik på at vurdere, hvordan den globale opvarmning potentielt vil påvirke resultaterne fundet i spørgsmål 3.

De fleste undersøgelser er foretaget i danske Væng Sø, hvor der blev foretaget biomanipulation i 1986-1988 samt igen i 2007-2008. Efter den første biomanipulation blev søen klarvandet, og undervandsplanter domineret af *Elodea canadensis* etablerede sig. Søen forblev i den klarvandede tilstand frem til 1997, hvor undervandsplanterne pludseligt forsvandt, og den uklare, fytoplankton-dominerede tilstand vendte tilbage. Fra 2009, efter den anden biomanipulation, blev søen igen klarvandet og domineret af *E. canadensis*.

Tætheden af bentiske makroinvertebrater blev fulgt i perioden fra 1988 til 2006, hvor den fluktuerede en del. I 1990, to år efter biomanipulationen, toppede tætheden af makroinvertebrater, hvilket især skyldtes, at antallet af chironomider var højt. Denne stigning i tætheden af makroinvertebrater skyldtes sandsynligvis reduceret prædationstryk fra brasen (*Abramis brama*) og skalle (*Rutilus rutilus*) samt øget dækningsgrad af undervandsplanter. Generelt var tætheden af makroinvertebrater højere i år med undervandsplanter end i år uden, hvilket delvist kunne skyldes det refugium fra fiskeprædation, som planterne udgør, og delvist at der i disse år blev fundet flere plantetilknyttede makroinvertebrater i bundprøverne.

I 1990 var tætheden af *Chironomus*-larver ca. 1400 ind. m^{-2} højere end den gennemsnitlige tæthed for hele perioden. Resultater fra bioturbationsforsøg med sediment fra Væng Sø viste, at en sådan stigning i antallet af *Chironomus*-larver medfører signifikant højere frigivelse af ammonium, SRP og totalfosfor fra sedimentet samt højere denitrifikation.

Analyser af stabile kul- og kvælstofisotoper blev efterfølgende foretaget på de bentiske makroinvertebrater (ethanol-konserverede), på zooplankton (konserveret med Lugol's opløsning) samt på skæl fra skalle. Både makroinvertebrater, cladoceer og cyclopoide copepoder havde højere $\delta^{13}C$

i år, hvor der fandtes undervandsplanter i søen. Vi forventer, at tætte bevoksninger af *E. canadensis* reducerede CO_2-koncentrationen i søen eller påvirkede flowet af ^{13}C-fattigt CO_2 fra sedimentet til vandfasen, hvilket har medført, at der i år med makrofyter var et højere $\delta^{13}C$ i fytoplanktonet og dermed også i højere trofiske niveauer. Fiskeskæl var kun tilgængelige fra et mindre antal år, men isotopsignalerne indikerede, at skallerne fouragerede mere littoralt i år med høj turbiditet, mens zooplankton udgjorde en større del af føden i år med klart vand.

I forbindelse med den anden biomanipulation i Væng Sø udsatte vi kunstige plantebede i søen, og jeg fulgte tætheden af plantetilknyttede makroinvertebrater på de kunstige planter. Tætheden af makroinvertebrater steg igennem hele året i 2007, mens den var lavere i september og oktober 2008 samt i 2009. Denne forskel i tætheder af makroinvertebrater var sandsynligvis forårsaget, direkte eller indirekte, af et højt prædationstryk fra 0^+ aborre (*Perca fluviatilis*) i 2008 samt i 2009, hvor aborrerne var større, og hvor klart vand kan have øget jagteffektiviteten. De kunstige planter understøttede en høj tæthed af makroinvertebrater og kan derfor være et nyttigt redskab til at øge tilgængeligheden af byttedyr for aborre, når rekoloniseringen af naturlig undervandsvegetation er forsinket efter biomanipulation og næringsstofreduktion. Potentielt kan dette øge væksten hos aborre og dermed medføre en højere rekruttering til det piscivore stadie.

For at belyse potentielle effekter af den globale opvarmning på samspillet mellem makroinvertebrater, planter og fisk sammenlignede vi makroinvertebratsamfund mellem Danmark og Uruguay. Makroinvertebraterne blev indsamlet fra kunstige, flydende planter og fra undervandsplanter, der var placeret i søer dækkende en trofisk gradient i begge lande. Tætheden af makroinvertebrater per gram plante var lavest i uruguayanske søer, hvor tætheden af små herbivore og omnivore fisk var høj. Flydende planter understøttede generelt højere tætheder af makroinvertebrater per gram plante end undervandsplanter, og denne forskel var størst i klart vand. Dette kunne skyldes, at det refugium fra fiskeprædation, som flydende planter yder i form af deres skyggevirkning, mister betydning, når sigtdybden mindskes.

Det kan konkluderes, at etableringen af undervandsplanter efter en reduktion i biomassen af zooplanktivore og benthivore fisk vil medføre højere tæthed af makroinvertebrater, til trods for at stærke kohorter af 0^+ aborre kan have en negativ effekt på tætheden af plantetilknyttede makroinvertebrater. Kunstige planter kan potentielt bruges som et nyttigt redskab i den indledende fase efter biomanipulation, da de øger tætheden af byttedyr for aborren, der dermed kan øge sin vækst og hurtigere nå det piscivore stadie. Lavere tætheder af plantetilknyttede makroinvertebrater fundet i subtropiske søer og en potentiel stigning i fisketætheden i tempererede søer som følge af den globale opvarmning indikerer dog, at tætheden af plantetilknyttede makroinvertebrater reduceres i et fremtidigt varmere klima.

3 Introduction

Shallow lakes are widely distributed and the most abundant lake type in the world (Wetzel 2001), and they form an important habitat for a variety of insect larvae and nymphs as well as for other macroinvertebrates. Especially macrophyte-covered areas may exhibit a high richness, biomass and density of macroinvertebrates (Scheffer 2004). Due to their shallowness these lakes can potentially support submerged macrophytes in the entire basin (Wetzel 2001); however, the distribution of macrophytes is to a large extent affected by competition with phytoplankton for nutrients, inorganic carbon and light (Sand-Jensen and Borum 1991; Søndergaard and Moss 1998).

At intermediate nutrient levels shallow temperate lakes may be in either of two alternative stable states - a clear water state dominated by submerged vegetation or a turbid state dominated by phytoplankton (Scheffer 1990; Moss 1990; Scheffer *et al.* 1993). The clear water state is stabilised by macrophytes through various positive feedback mechanisms (Jeppesen *et al.* 1998). Perch (*Perca fluviatilis* L.) and northern pike (*Esox lucius* L.) are more efficient than for example roach (*Rutilus rutilus* L.) and bream (*Abramis brama* L.) in feeding among the vegetation (Winfield 1986; Diehl 1988; Grimm and Backx 1990) and, furthermore, macrophytes increase sedimentation, stabilise the sediment and affect nutrient dynamics (Barko and James 1998). Macrophytes also serve as a refuge for phytoplankton-grazing zooplankton (Timms and Moss 1984; Schriver *et al.* 1995; Lauridsen *et al.* 1996).

In contrast, the turbid state is stabilised by high densities of phytoplankton leading to reduced availability of light for submerged macrophytes and by benthivorous fish that resuspend algae (Roozen *et al.* 2007) and sediment, release nutrients (Meijer *et al.* 1990; Breukelaar *et al.* 1994; Tarvainen *et al.* 2005) and may prevent macrophyte growth (Meijer *et al.* 1990). Moreover, planktivorous fish stabilise the turbid state by reducing zooplankton densities, rendering top-down control on phytoplankton less likely (Shapiro and Wright 1984; Benndorf 1990; Jeppesen *et al.* 1990a; Hansson *et al.* 1998; Meijer *et al.* 1999). At the same time strong competition from planktivorous cyprinids for zooplankton can reduce the growth of small perch and thus limit the recruitment to its later piscivorous stage (Persson and Greenberg 1990b).

The existence of two alternative stable states has made eutrophied shallow lakes a particular target for various attempts of lake restoration aiming at triggering a shift from the turbid state to a clear water state stabilised by submerged macrophytes. Methods for restoring lake water quality include removal of sediment, oxidation of bottom water, aluminium addition, removal of benthivorous and zooplanktivorous fish, and stocking of piscivorous fish (Hansson *et al.* 1998; Søndergaard *et al.* 2007). The expression "biomanipulation" covers several methods, but will in this thesis represent removal of benthivorous and zooplanktivorous fish. Biomanipulation is the most commonly used lake restoration method in Denmark and the Netherlands, countries dominated by shallow lakes (Søndergaard *et al.* 2007). It has proved successful for creating the shift from turbid to clear water and providing conditions for stabilising the clear water state, although the effects typically last less than ten years (Hansson *et al.* 1998; Søndergaard *et al.* 2007; Søndergaard *et al.* 2008).

Freshwater macroinvertebrates comprise a functionally and taxonomically diverse group, which may obtain high abundance in shallow lakes, and they are recognised as playing an important role in linking the benthic and the pelagic as part of the food web (Vander Zanden and Vadeboncoeur 2002; Jones and Waldron 2003). Macroinvertebrates constitute an important food source for various fish species (Persson 1983a; Persson 1983b; Lammens *et al.* 1985; Sierszen, McDonald, and Jensen 2003). Moreover, the opportunity to feed on macroinvertebrates during certain life stages may enable fish to reach the piscivorous stage (Allen 1935), and for zooplanktivorous fish macroinvertebrates act as a supplement to pelagic resources (Jeppesen *et al.* 1997; Vander Zanden and Vadeboncoeur 2002). At the same time macroinvertebrates are also involved in the recycling of nutrients, both across the sediment interface (Gallepp 1979; Tátrai 1986; Andersen and Jensen 1991; Vanni 2002) and among macrophytes (Kairesalo and Koskimies 1987; Underwood 1991).

Areas with submerged macrophytes may exhibit higher numbers or a higher biomass of macroinvertebrates than sparsely vegetated areas (Hargeby *et al.* 1994; Scheffer 2004) and, therefore, shallow lakes can potentially support a high production of macroinvertebrates. Macroinvertebrates may enhance macrophyte growth by grazing epiphyton, but this positive interaction may vanish if fish predation reduces the number of grazing macroinvertebrates (Brönmark 1989; Brönmark and Vermaat 1998; Jones and Sayer 2003). Thus, due to the complex interactions between macrophytes, macroinvertebrates and fish it is a challenge to predict how macroinvertebrates are affected by biomanipulation and how they influence the recovering processes of the lakes.

The knowledge we acquire today may not be directly applicable in the future considering the predictions by the Intergovernmental Panel on Climate Change (IPCC 2007) on future climate change. It is expected that climate change may have various impacts on shallow water bodies (Mooij *et al.* 2005; Jeppesen *et al.* 2007). A warmer climate could result in higher densities of small omnivorous fish (Teixeira-de Mello *et al.* 2009) and increase the risk of triggering a shift to or stabilising an already existing turbid state (Jeppesen, Søndergaard, and Jensen 2003; 2009). It may also potentially benefit the growth of free-floating plants and thereby promote a third stable state of shallow lakes (Scheffer *et al.* 2003).

4 Objectives and approach

The general aim of this thesis was to examine how biomanipulation affects macroinvertebrate communities and how macroinvertebrates potentially influence lake restoration processes. Seen in the light of the ongoing climate change, I also investigated how macroinvertebrate communities in a future warmer climate might differ from those occurring today. Four main questions were formulated and sought answered:

1) How do reduced biomass of benthivorous and zooplanktivorous fish and expanding coverage of submerged macrophytes affect benthic macroinvertebrate communities?

- **Hypothesis:** Decreased biomass of benthivorous fish will reduce the predation pressure on macroinvertebrates and lead to higher density of benthic macroinvertebrates. This predation risk will be reduced by an expanding coverage of macrophytes acting as a refuge and potential part-time foraging area for benthic macroinvertebrates.

2) How do benthic chironomids affect release of nutrients from the sediment in shallow lakes?

- **Hypothesis:** Through bioturbation and bio-irrigation benthic chironomids stimulate the microbial processes and enhance the release of nutrients from the sediment. Consequently, a reduced predation leading to higher density of macroinvertebrates may enhance the nutrient release, but may potentially be modulated or counteracted by enhanced benthic algae growth due to improved light conditions.

3) How are macroinvertebrate communities reacting to establishment of macrophyte beds and how do changes in fish community and environmental parameters following biomanipulation affect these plant-associated macroinvertebrates?

- **Hypothesis:** Macrophyte beds will provide an important habitat for macroinvertebrates that consequently will increase in density. While visually hunting fish predators, such as perch, may benefit from clear water and reduced competition after biomanipulation and thus prey strongly on plant-associated macroinvertebrates with a potential negative impact on macroinvertebrate densities as result.

4) How do interactions between macroinvertebrates, plants and fish in lakes in warmer climates differ from those between macroinvertebrates, plants and fish in temperate lakes today?

- **Hypothesis:** Warm water lakes are expected to support higher densities of smaller bodied fishes and to exhibit higher turbidity. Higher fish density is hypothesised to reduce the density of plant-associated macroinvertebrates, whereas turbidity is expected to promote the coexistence of macroinvertebrates and their fish predators. Due to the higher fish predation and fast fish reproduction it is expected that warming of lakes will reduce the chances of enhancing macroinvertebrate density through biomanipulation.

These questions were sought answered by examining macroinvertebrates found in sediment samples collected over an 18-year period covering a shift from a clear water state to turbid state and by studying macroinvertebrate communities on artificial plants positioned in the lake before and after biomanipulation, including the time of the shift from a turbid to a clear water state. Bioturbation experiments were conducted in the laboratory on intact sediment cores. Possible impacts of climate change were evaluated by comparing macroinvertebrate communities found on artificial plants established in temperate (Danish) and subtropical (Uruguayan) lakes.

5 Benthic macroinvertebrates

5.1 Effects of biomanipulation on communities of benthic macroinvertebrates

Macroinvertebrates serve as an important food source for a number of fish species such as perch (Persson 1983b), roach (Persson 1983a) and bream (Lammens *et al.* 1985; Persson and Hansson 1999), and since fish can have a negative impact on the densities of benthic macroinvertebrates (Lammens *et al.* 1985) changes in fish biomass were expected to reduce the predation pressure on benthic macroinvertebrates whose density might therefore increase.

A complete removal of planktivorous fish can result in dominance of predatory macroinvertebrates (Wissel and Benndorf 1998); however, a 50-80% reduction of the fish stock is more common than total elimination (Lammens 1999). In North European lakes bream and roach have been the target fish for removal in connection with biomanipulation (Søndergaard *et al.* 2007), and a higher density or biomass of benthic macroinvertebrates has often been observed shortly after the changed composition of the fish stock (Svensson, Bergman, and Andersson 1999; Leppä, Hämäläinen, and Karjalainen 2003; Manuscript 1). In Lake Væng, the density of benthic macroinvertebrates reached a peak two years after the biomanipulation (Fig. 1). This peak was partly due to a significantly higher density of chironomids, encompassing Tanypodinae, Tanytarsini, *Chironomus* sp. and Chironomini (others than *Chironomus* sp.). The higher density of macroinvertebrates is likely a result of reduced predation pressure from fish, and the fact that also the truly benthic *Chironomus* sp. was found in higher density in 1990 supports that release from fish predation might have been a determining factor. Also the negative correlations found between total density of macroinvertebrates and of chironomids and between CPUE of bream and roach indicate an effect of fish predation, although CPUE values of bream and roach were not selected in the final model (Manuscript 1). Our finding thus supports the results of Leppä (2003). In general, a decrease in predation pressure from fish can both be mediated by the lower biomass of benthivorous fish and by an increased refuge effect created by macrophytes (Gilinsky 1984; Diehl 1988).

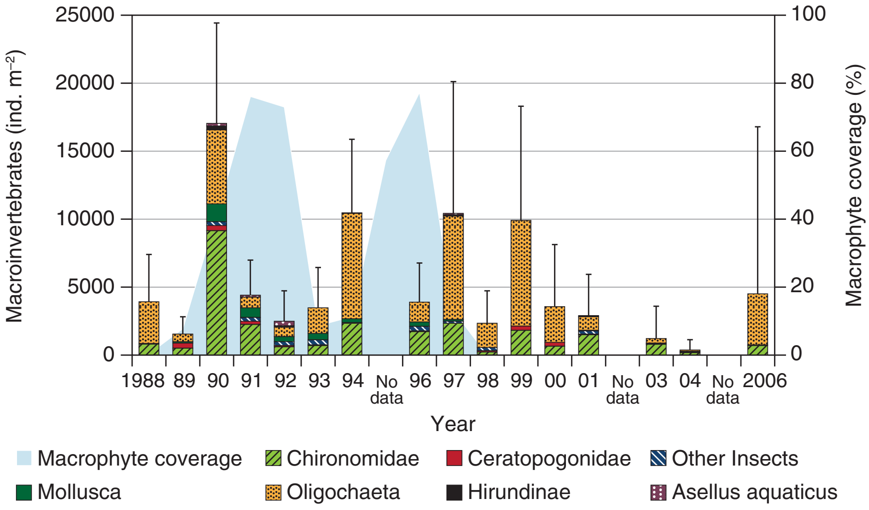


Figure 1. Mean densities (±S.D.) of benthic macroinvertebrates collected in Lake Væng during 1988 to 2006. Benthic macroinvertebrates were not collected in 1995, 2002 and 2005. Estimates of macrophyte coverage during the periods prior to sampling of benthic macroinvertebrates are provided on the right y-axis. (This figure is modified from Manuscript 1).

Bottom-up control may be important for benthic macroinvertebrate communities and production of benthic macroinvertebrates also depends on primary production (Rasmussen and Kalff 1987; Specziár and Vörös 2001). A decrease in phytoplankton production after biomanipulation will therefore most probably lead to lower biomass or density of benthic macroinvertebrates unless release of predation is an overriding factor. However, in Lake Væng we found that the density of chironomids was negatively correlated with chlorophyll *a* (Chl *a*) (Manuscript 1) and resource limitation was thus not of key importance.

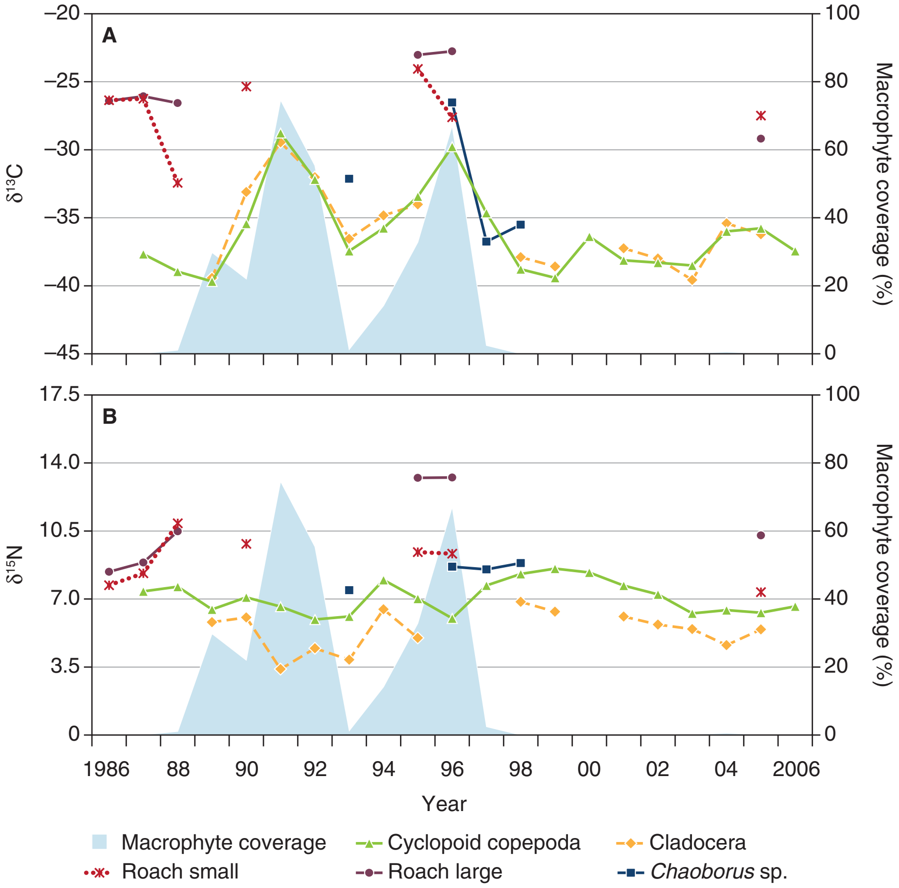
Members of the subfamily Orthocladiinae appeared in high numbers in 1991 and to some extent also in 1996. In both years coverage of submerged macrophytes was high and the Orthocladiinae species occurring were likely plant-associated rather than truly benthic (Manuscript 1). In support of this, Orthocladiinae was found in high abundances on artificial plants placed in Lake Væng during the years 2007 to 2009 (Manuscript 2). Many species of Orthocladiinae are fast colonisers, enabling them to benefit from improved habitat and food conditions (Pinder 1992). Other groups of macroinvertebrates, such as *Asellus aquaticus* (L.), leeches and snails, were also found in higher densities in years with macrophytes; thus, macrophytes did have a positive effect on the density and taxon richness of the benthic macroinvertebrate community (Fig. 1). *Asellus aquaticus* may be slow in colonising but is associated with established macrophyte beds (Hargeby 1990).

Higher biomass and density of benthic macroinvertebrates have been found after biomanipulation in a lake where macrophyte coverage was scarce (Leppä *et al.* 2003), but densities of macroinvertebrates have also been shown to increase when submerged macrophytes expand their coverage (Hargeby *et al.* 1994). In conclusion, our results revealed a positive effect of macrophyte coverage on density and taxon richness of macroinvertebrates as well as strong indications of a negative impact of bream and roach on macroinvertebrate density. However, a clear distinction between the effects of lower biomass of benthivorous fish, refuge provided by macrophytes and the general positive effect of macrophytes on benthic macroinvertebrate density could not be made; most likely a combined effect of all three factors was responsible for the results.

5.2 Benthic macroinvertebrates and trophic interactions described by stable isotope analysis

Stable isotope analysis is often used to described trophic interactions in food webs (Post 2002; Vander Zanden and Fetzer 2007). The isotope $\delta^{13}C$ has been used to describe the carbon source allowing determination of whether the animal fed in the pelagic, the profundal or in the littoral zone (France 1995; Vander Zanden and Rasmussen 1999). We analysed stable isotope ratios for a variety of benthic macroinvertebrates as well as for cladocerans and cyclopoid copepods (Manuscript 1). Benthic macroinvertebrates and zooplankton were collected in the period 1986-2006 and preserved in ethanol and Lugol's solution, respectively. We found higher $\delta^{13}C$ in invertebrates collected in years with macrophyte presence in Lake Væng, and since this pattern was apparent for a variety of invertebrate taxa from different habitats we argue that the shift was not caused by changes in selected food source selected, but rather by a change in the $\delta^{13}C$ baseline.

Figure 2. δ^{13}C (**A**) and δ^{15}N (**B**) of copepods, cladocerans, and roach scales from Lake Væng plotted together with macrophyte coverage for the 30-day period prior to sampling of copepods and cladocerans. (This figure is modified from Manuscript 1).



Dense beds of *Elodea canadensis* (Michx) established in the lake after the biomanipulation (Lauridsen, Jeppesen, and Søndergaard 1994) and may have affected the δ^{13}C of phytoplankton, by either lowering total CO_2 concentrations or by taking up proportionally more of the ^{13}C-depleted CO_2 released from respiratory processes in the sediment. CO_2 concentrations may be low inside dense macrophyte beds (Jones, Hardwick, and Eaton 1996) and changes in CO_2 concentrations or in CO_2 sources may lead to changes in the δ^{13}C of primary producers (Peterson and Fry 1987), including the phytoplankton. Since the δ^{13}C of consumers at higher trophic levels depends on the δ^{13}C of the primary producers (Deniro and Epstein 1978; Peterson and Fry 1987; Post 2002), a change in δ^{13}C of phytoplankton would be detected as a difference in δ^{13}C of invertebrates – as observed in our study of Lake Væng (Fig. 2) (Manuscript 1). Thus, macrophytes affect macroinvertebrate communities in several ways and also indirectly the isotope signal of the macroinvertebrates.

Stable isotope analyses are relevant for paleolimnological studies of former HCO_3^- concentrations in lakes as an indicator of submerged macrophyte productivity (Herzschuh *et al.* 2010). The findings in our study have important implications for such studies since isotope analysis of macroinvertebrate remains found in the sediment likely will provide additional knowledge about macrophyte coverage and carbon dynamics. Recent sediment studies by T. A. Davidson concurs with these findings (unpublished).

Higher δ^{13}C of macroinvertebrates will result in higher δ^{13}C of the fish feeding on the macroinvertebrates. However, since fish are motile and have a relatively high longevity their δ^{13}C will show an integrated signal covering food sources from different habitats, especially in the complex food web of shallow lakes (Jones and Waldron 2003), and a longer time period (Perga and Gerdeaux 2005). In our study only relatively few data were available on $\delta^{13}C$ of roach and, therefore, it was not possible to validate whether the $\delta^{13}C$ of roach followed the same pattern as for zooplankton. This would be expected for small-sized roach.

Acknowledging the limitations of the data on the stable isotope signal from roach scales we found indications of a shift in food source for especially small roach when the lake shifted from a turbid to a clear water state. The change in $\delta^{13}C$ and the increase in $\delta^{15}N$ indicate that roach feed higher in the food web after Lake Væng shifted to a clear water state (Fig. 2). With roach positioned approximately one trophic level above cyclopoid copepods, it is likely that zooplankton contributed more to the diet. This is also expected since the biomass of zooplankton had increased in the lake at that time (Jeppesen *et al.* 1990b). In turbid lakes where the fish stock and thus competition for zooplankton is high, roach are expected to feed more in the littoral (Jeppesen *et al.* 2006; Lund *et al.* 2010) and potentially include more detritus and plant material in their diet (Tolonen *et al.* 2000). Later in the study period (1996, 1997) and after several years with macrophyte presence, the $\delta^{15}N$ signal of large roach was higher than during the turbid period. In 1996 and 1997 the $\delta^{15}N$ of large roach was approximately two trophic levels (7‰) above zooplankton (Fig. 2); thus, large roach probably fed even higher up the food web – potentially on *Chaoborus* sp., *Leptodora kindtii* (Focke) or other predatory macroinvertebrates. It is likely that large roach included more macroinvertebrates in their diet during the years with abundant macrophytes, both because macrophytes can harbour high densities of macroinvertebrates (Manuscript 2), but also because food competition, from for example bream, for benthic macroinvertebrates was lower.

5.3 Bioturbation and the effect of macroinvertebrates on nutrient recycling

Macroinvertebrates influence nutrient translocation by increasing the exchange of nutrients across the sediment-water interface. Benthic macroinvertebrates such as chironomid larvae excrete nutrients (Gallepp 1979; Tátrai 1986) and stimulate microbial activity in the sediment via bioturbation and bio-irrigation (Andersen and Jensen 1991; Svensson and Leonardson 1996).

Sediment from Lake Væng is rich in organic matter (Lauridsen, Jeppesen, and Andersen 1993; Boll unpubl. data) and benthic macroinvertebrates were expected to influence the mineralisation processes. Chironomids also clearly increased the release of ammonium, soluble reactive phosphorus (SRP) and total phosphorus (TP) in the bioturbation experiment (Box 1, Table 1, Fig. 3). Chironomid activity can increase the oxygen uptake in the sediment (Andersen and Jensen 1991; Svensson and Leonardson 1996) due to respiration as well as increased microbial mineralisation. Increased mineralisation leads to release of ammonium (Tátrai 1982; Tátrai 1986; Andersen and Jensen 1991) as well as of phosphate (Gallepp 1979; Andersen and Jensen 1991). I found only low ammonium release from reference sediment cores, while there was an efflux of nitrite and nitrate, most likely due to nitrification. In cores with additional chironomids ammonium release was recorded, and in spring there was a tendency to lower release

Table 1. Repeated measures ANOVA was applied to flux data from bioturbation experiment. Before analysis data were transformed $[(\sqrt{|x|}) * \text{sign}(x)]$ to approach normality.

Factor	d.f.$_{(num,den)}$	NH_4	NO_3	PO_4	TP
Season (S)	1,12	0.06	97.83 ****	45.00 ****	62.73 ****
Treatment (T)	1,12	98.21****	24.68 ***	60.71 ****	27.67 ***
S * T	1,12	0.04	24.63 ***	0.68	0.55
Time (Ti)	3,36	11.66****	21.76 ****	21.33 ****	11.35 ****
Ti * S	3,36	11.82****	7.38 ***	9.51 ****	26.59 ****
Ti * T	3,36	6.48**	8.35 ***	13.03 ****	4.90 **
Ti * S * T	3,36	3.21*	2.53	11.59 ****	6.38 **

Significant results are identified by:
*$P<0.05$; **$P<0.01$; ***$P<0.001$; ****$P<0.0001$

from or even an uptake (week 1) of nitrite and nitrate in the sediment. Uptake or low fluxes of nitrite and nitrate from the sediment are expectedly a result of enhanced denitrification due to the burrowing activity of the chironomids (Svensson and Leonardson 1996).

Biomass of chironomids and temperature have shown to be important factors affecting the exchange of nutrients (Gallepp 1979; Tátrai 1986; Andersen and Jensen 1991). In my experiment the density of chironomids was lower in summer (20º C; +1400 *Chironomus* larvae m^{-2}) than in spring (10º C; +2800 *Chironomus* larvae m^{-2}), but despite the higher densities of chironomids in spring release of SRP was lower, indicating that temperature also have an effect on the release of SRP (Fig. 3). Also the flux of nitrite-nitrate was lower in spring for both cores with and without extra chironomids and it thus seems likely that also nitrification processes have been affected by temperature. Lower nitrification rates at lower temperatures have been observed in other bioturbation experiments as well (Svensson 1998).

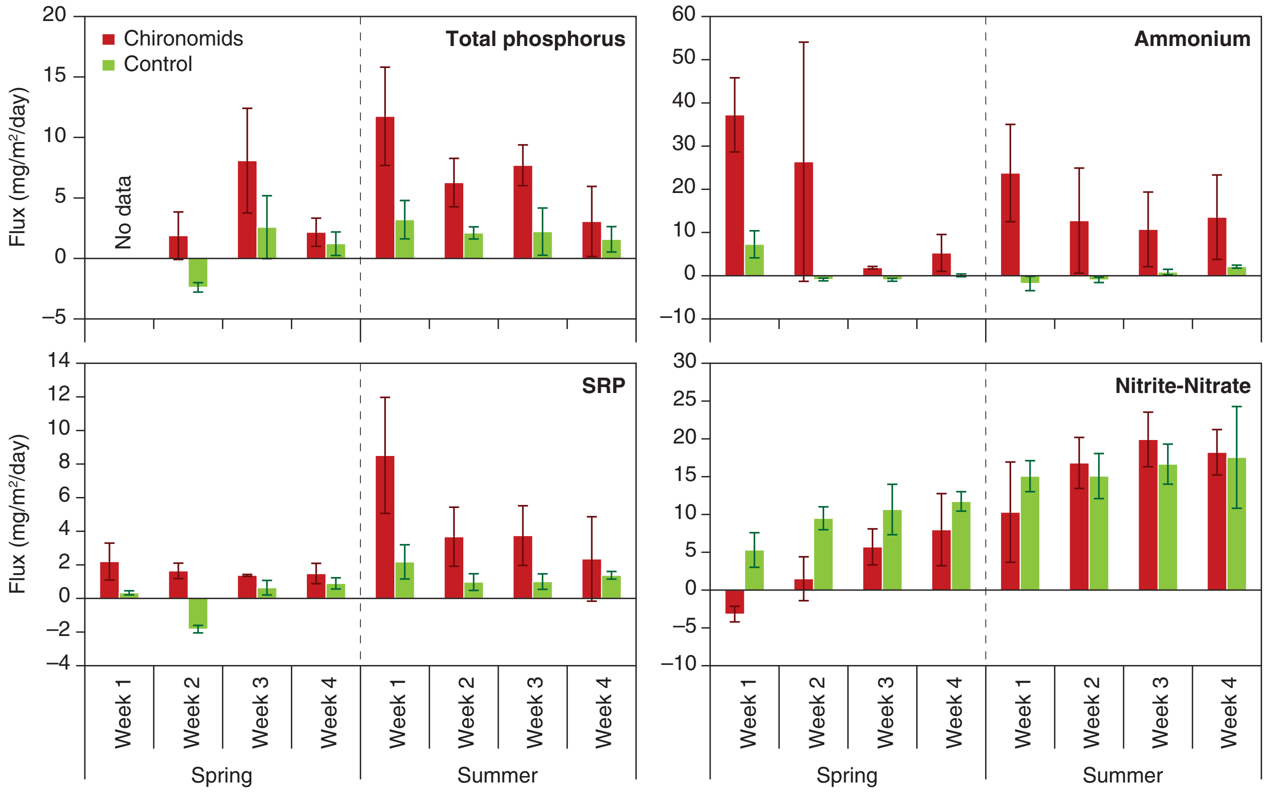


Figure 3. Results from bioturbation experiment with sediment cores collected from Lake Væng. Spring experiment was conducted at 10° C and summer experiment at 20° C. Chironomid densities were ~2800 ind. m^{-2} (spring) and ~1400 ind. m^{-2} (summer). Fluxes are shown as mean ±S.D.

Effects of biomanipulation on macroinvertebrate-mediated nutrient fluxes and effects of macroinvertebrate-mediated nutrient fluxes on lake recovery processes are complicated study issues. Benthic macroinvertebrates clearly have an impact on nutrient fluxes in shallow lakes (Gallepp 1979; Tátrai 1986; Andersen and Jensen 1991; Svensson and Leonardson 1996), as also seen in this study, and thus contribute to the in-lake concentration of mobilised nutrients, but the magnitude of the change following biomanipulation is uncertain since it depends on the activity and density of the macroinvertebrates as well as on pelagic and benthic primary production and sediment composition. Densities of benthic macroinvertebrates in lakes generally fluctuate from year to year, which was also the case in Lake Væng (Manuscript 1).

In Lake Væng a peak in density of chironomids occurred two years after the biomanipulation (Manuscript 1) when *Chironomus* sp. density reached approximately 1700 m^{-2} and thus was about 1450 m^{-2} higher than the average density during the whole period. Results from the bioturbation experiment showed that an increase in the density of *Chironomus* larvae by 1400 m^{-2} will significantly increase nutrient fluxes. Thus, the release of ammonium, SRP and total phosphorus, caused by bioturbation from chironomids, has expectedly increased after the biomanipulation. Yet, increased denitrification rates may also be expected as a result of the increase in bioturbation; thus, chironomids may have had both positive and negative impacts on nutrient availability to the phytoplankton and consequently for the recovering processes of the lake. However, although the density of benthic macroinvertebrates may increase after biomanipulation this is often short-lived (Leppä *et al.* 2003; Manuscript 1) and an increase in nutrient fluxes is expectedly restricted to years with peak densities of benthic macroinvertebrates.

Relative to biomanipulation changes in nutrient fluxes seem more likely to be influenced by an expanding macrophyte coverage and a severe reduction in the biomass of benthivorous fish. A dense stock of benthivorous fish can consume large amounts of detritus (Tolonen *et al.* 2000) and increase nutrient concentrations in the lake water (Breukelaar *et al.* 1994; Tarvainen *et al.* 2005). Increased Secchi depth and thus improved light conditions, as a consequence of biomanipulation, may also lead to increased benthic algae production (Hansson 1992; Liboriussen and Jeppesen 2003; Vadeboncoeur *et al.* 2008). An increase in the production of benthic algae can reduce fluxes of phosphorus from the sediment to the water column (Carlton and Wetzel 1988; Hansson 1990) and will therefore also counteract the release of phosphorus mediated by a larger chironomid population following biomanipulation. Thus, it is concluded that chironomids may play an important role for mineralisation processes in lake sediment. However, in relation to biomanipulation enhanced release of nutrients, due to higher densities of chironomids, is considered to be of minor importance when compared to the number of feedback effects leading to a reduction in lake water nutrients following biomanipulation, including the effect of reduction in benthivorous fish, increased growth of macrophytes and of benthic algae.

Box 1 Bioturbation Experiment

Material

Photos: Thomas Boll

The sediment of Lake Væng (16 ha, depth: average 1.2 m, max 1.9 m) consists of soft, organic rich mud which is inhabited by benthic macroinvertebrates such as Chironomidae, Ceratopogononidae and Oligochaeta (Manuscript 1). Bioturbation and bio-irrigation of these animals affect microbial processes in the sediment and nutrient translocation across the sediment-water interface. To estimate potential effects of *Chironomus* larvae on nutrient dynamics in Lake Væng bioturbation experiments were conducted using intact sediment cores from the lake.

Methods

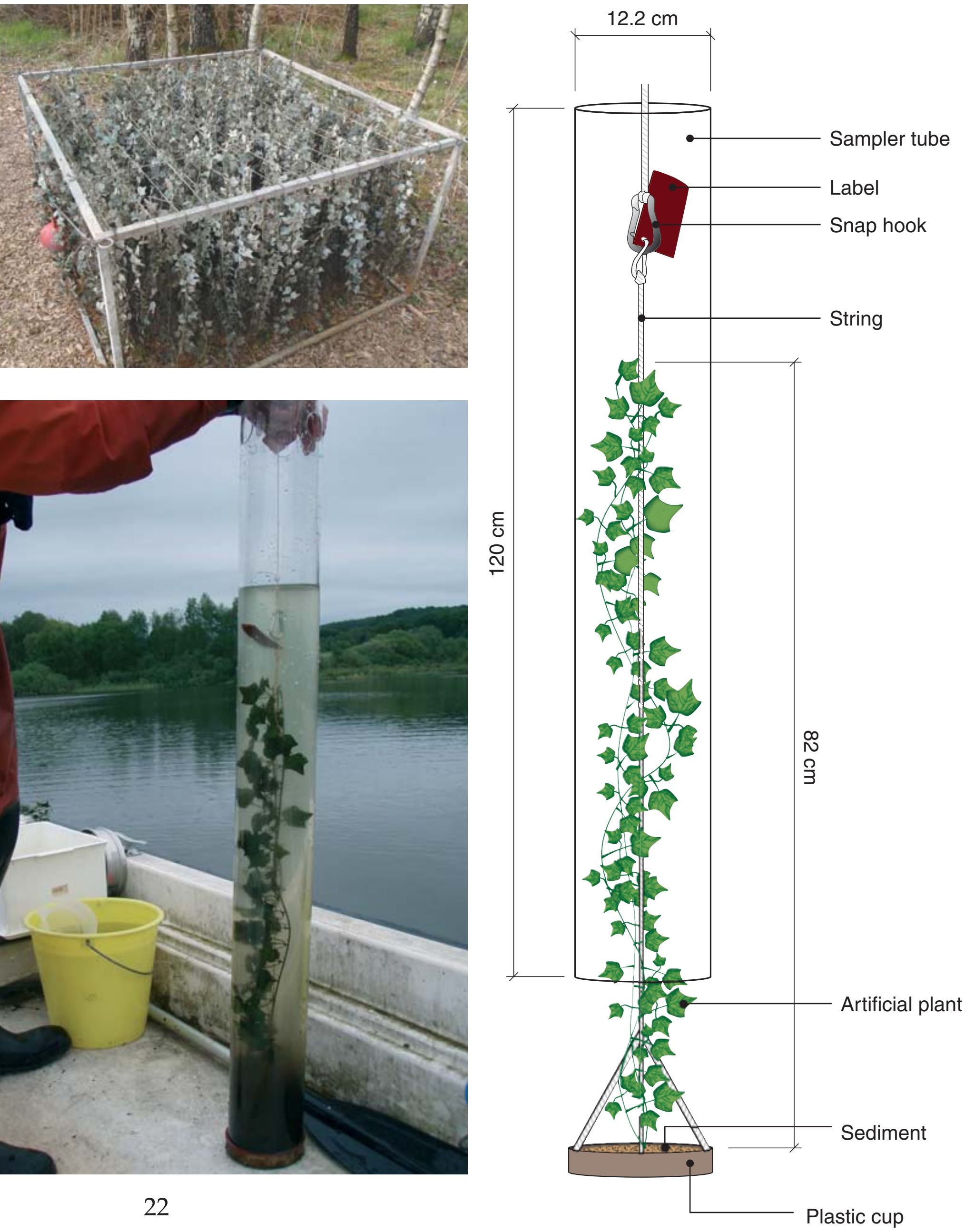
In late April and late July 2007 eight sediment cores were taken in Kajak tubes from an area of Lake Væng with ~1.5 m water depth. Each Kajak tube contained 20 cm of sediment and the tubes were placed below water in a tank with artificial lake water. Each tube was covered with a net and magnetic stirring facilitated the exchange of water from the tube to the tank. In addition, water in the tank was aerated to create water currents and to ensure that the water was fully oxygenated. Incubation was undertaken in the dark and at a constant temperature of 10° C (spring) and 20° C (summer). After one day six larvae (spring) or three larvae (summer) of *Chironomus plumosus* (L.) were added to half of the tubes giving four replicates with “natural densities” of benthic macroinvertebrates and four replicates with “natural densities” + extra chironomids (~2800 chironomids m^{-2} (spring); ~1400 chironomids m^{-2} (summer)). The experiment ran for four weeks and each week sediment cores were isolated, and the water level in each tube was adjusted to equal volumes (125 ml). Flux measurements were conducted over 24 hours.

6 Plant-associated macroinvertebrates

6.1 Effects of macrophytes and periphyton on densities of macroinvertebrates

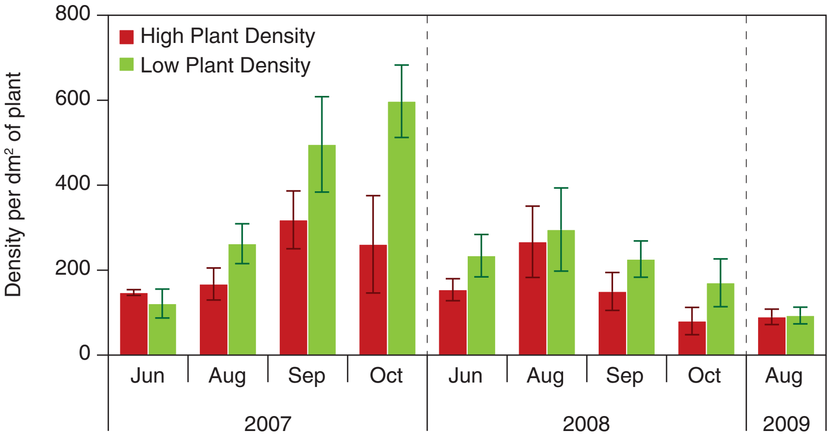
Macrophytes provide an important habitat for macroinvertebrates and, as mentioned above, some of the macroinvertebrates appearing in sediment samples following the biomanipulation are likely associated with macrophytes since they only occur in years with presence of macrophytes (Manuscript 1). Gastropoda was only found in years with macrophytes and so was Orthocladiinae. Species of Gastropoda, like many other macroinvertebrates, feed on settled material and epiphytic algae from the surface of the macrophytes (Cattaneo 1983; Cattaneo *et al.* 1998; James, Hawes, and Weatherhead 2000). Also for chironomids, including Orthocladiinae, the production and quality of epiphyton are important for growth (Pinder 1992). In order to study the effect of macrophytes on macroinvertebrate composition and density we used open mesocosms with artificial plants in Danish Lake Væng (Fig. 4) (Manuscript 2) as well as artificial free-floating and submerged plants in a set of Danish and Uruguayan lakes (Manuscript 3).

Figure 4. Artificial plant bed used in lake Væng (upper left). One full sample including artificial plant, water column and sediment (lower left). Detailed drawing of artificial plant and sampler used in collecting macroinvertebrates (right).



Periphyton production in Danish lakes may increase rapidly in spring after ice-out and reach a maximum of 112 mg Chl *a* m^{-2} $month^{-1}$ (Liboriussen and Jeppesen 2009). Our experiment in Lake Væng did not cover the spring period and growth of periphyton was restricted to the period from mid-April to October. In this period periphyton biomass on the artificial plants increased from 1-2 µg Chl *a* cm^{-2} (equivalent to 10-20 mg m^{-2}) in June to 6-7 µg Chl *a* per cm^{2} (equivalent to 60-70 mg m^{-2}) in September and October in both 2007 and 2008 (Manuscript 2), and thus did not reach similar high growth rates as those occurring in spring in Danish Lake Torup (Liboriussen and Jeppesen 2009). Periphyton biomasses in Lake Væng were generally lower than those found by Liboriussen & Jeppesen (2009) but similar to biomasses of periphyton found in a nutrient enrichment experiment conducted in Lake Pedina in Turkey (Özkan *et al.* 2010). A collapse in periphyton biomass similar to what was observed in May in Lake Torup was not found in our experiment where periphyton biomass increased throughout the summer.

Figure 5. Densities of macroinvertebrates collected in June-October in 2007 and 2008 and in August in 2009 from artificial plant beds in Lake Væng. Densities are shown per dm^2 of plant surface (mean ± S.D.; n=3). (From Manuscript 2).

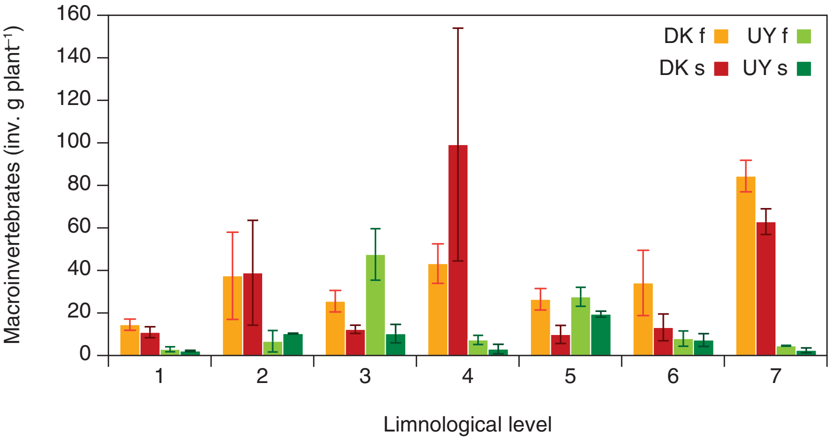


Coinciding with the increase in periphyton biomass in 2007 we found an enhanced density of macroinvertebrates, and a similar increase was recorded in the first two sampling rounds in 2008 (Fig. 5). This suggests that macroinvertebrate colonisation and development mainly depended on an increase in periphyton production during the first part of the study period (Manuscript 2).

Grazing macroinvertebrates can also reduce epiphyton biomass (Cattaneo 1983; Underwood, Thomas, and Baker 1992), and several studies have demonstrated a cascading effect from fish through changes in abundance of grazing macroinvertebrates to the biomass of epiphyton. The ultimate consequence of enhanced fish abundance will be reduced macrophyte growth since increased epiphyton biomass entails shading of the macrophytes (Brönmark 1989; Underwood *et al.* 1992; Brönmark and Vermaat 1998; Jones and Sayer 2003). Conversely, a reduced fish stock after biomanipulation leading to higher density of grazing macroinvertebrates may facilitate macrophyte growth and thereby help stabilising a clear water state (Jones and Sayer 2003; Burks *et al.* 2006). In our study of Lake Væng we did not find higher densities of plant-associated macroinvertebrates after the biomanipulation, rather several groups decreased in density (Manuscript 2). One exception was the molluscs, mainly snails, that occurred in higher densities in 2008 than in 2007, but even though snails are effective in reducing epiphyton biomass (Brönmark 1989), we found no interannual differences in periphyton biomass. This might reflect that a large proportion of the snails was juveniles (T. Boll, personal observation). However, periphyton biomass is also affected by several other factors such as nutrients (Beresford and Jones 2010; Özkan *et al.* 2010), light (Liboriussen *et al.* 2005) and total grazer biomass.

Also plant type and structural complexity influence the abundance and taxon richness of plant-associated macroinvertebrates (Cremona, Planas, and Lucotte 2008; van de Meutter, Cottenie, and DeMeester 2008); however, we found no difference in genus richness between macroinvertebrates on artificial submerged plants and free-floating plants (Manuscript 3). Still, free-floating plants generally exhibited higher densities of macroinvertebrates (Fig. 6) and this difference was expected to be mediated by fish predation, as discussed in subsequent sections. In some lakes, though, submerged plants harboured higher densities of macroinvertebrates, coinciding with high average periphyton biomass on the plants, thus supporting the assumption that periphyton may occasionally be important for the distribution and density of macroinvertebrates (Manuscript 3).

Figure 6. Densities of macroinvertebrates (ind. g plant^{-1}) found on artificial free-floating (f) and submerged (s) plants positioned in Danish (DK) and Uruguayan (UY) lakes. Limnological level covers lake characteristica, such as characterised including size, nutrient concentrations, physico-chemical variables, and macrophyte coverage, that were used to pair lakes in Uruguay and Denmark. Error lines show ±1 S.D. (From Manuscript 3).



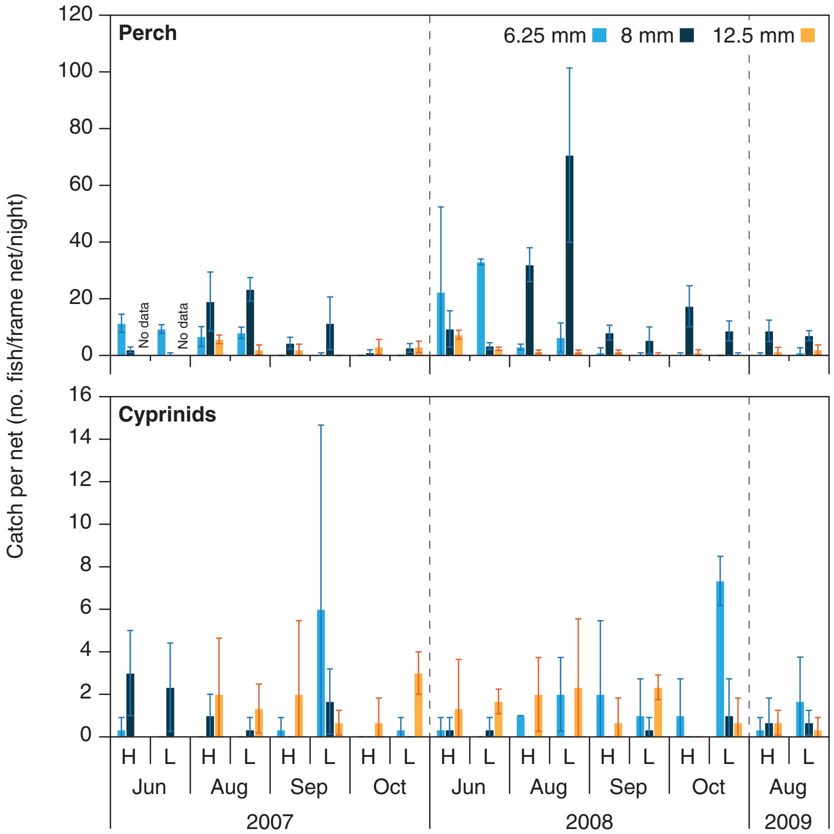
The high densities of macroinvertebrates found on the artificial plants in Lake Væng further confirm the positive role of macrophytes and their associated epiphytic community in determining the abundance of macroinvertebrates. The density of plant-associated macroinvertebrates was approximately 342,200 and 133,100 ind. m^{-2} of bottom at high and low plant density, respectively, (Manuscript 2), which was much higher than the mean densities of 3,548 ind. m^{-2} of benthic macroinvertebrates found in Lake Væng during 1998-2006 when submerged macrophytes were absent (Manuscript 1). This underlines the importance of the establishment of submerged vegetation following biomanipulation for the abundance of macroinvertebrates.

6.2 Interactions between plant-associated macroinvertebrates, fish and macrophytes

Besides providing macroinvertebrates with food resources (e.g. epiphyton) macrophytes also affect interactions between macroinvertebrates and their fish predators (Crowder and Cooper 1982; Gilinsky 1984; Diehl 1988; Diehl and Kornijów 1998). In the artificial plant beds in Lake Væng (Fig. 4) we also studied the effects of fish community changes on plant-associated macroinvertebrates. Macrophyte coverage was kept constant while fish community changed as result of the manipulation of the fish stock (Manuscript 2).

Total density of plant-associated macroinvertebrates declined after the biomanipulation of Lake Væng (Fig. 5), and predation from leeches may have been a contributory cause (Manuscript 2). However, high densities of young of year (YOY) fish often occur within the first years after biomanipulation (Hansson *et al.* 1998) and this was also the case for perch in Lake Væng (Fig. 7) (Manuscript 2). Thus, a heavy predation pressure from a strong cohort of YOY perch likely explains the lower macroinvertebrate density in 2008, while a combination of high predation pressure from YOY perch and lower turbidity is argued to be the reason behind the observed lower density of plant-associated macroinvertebrates in 2009. The hunting efficiency of perch is reduced by high phytoplankton turbidity, as seen for adult perch (Radke and Gaupisch 2005), and therefore the lower turbidity in 2009 might have enhanced the negative impact of perch on plant-associated macroinvertebrates. Higher predation efficiency by perch was supported by the fact that they had a larger body size in 2009.

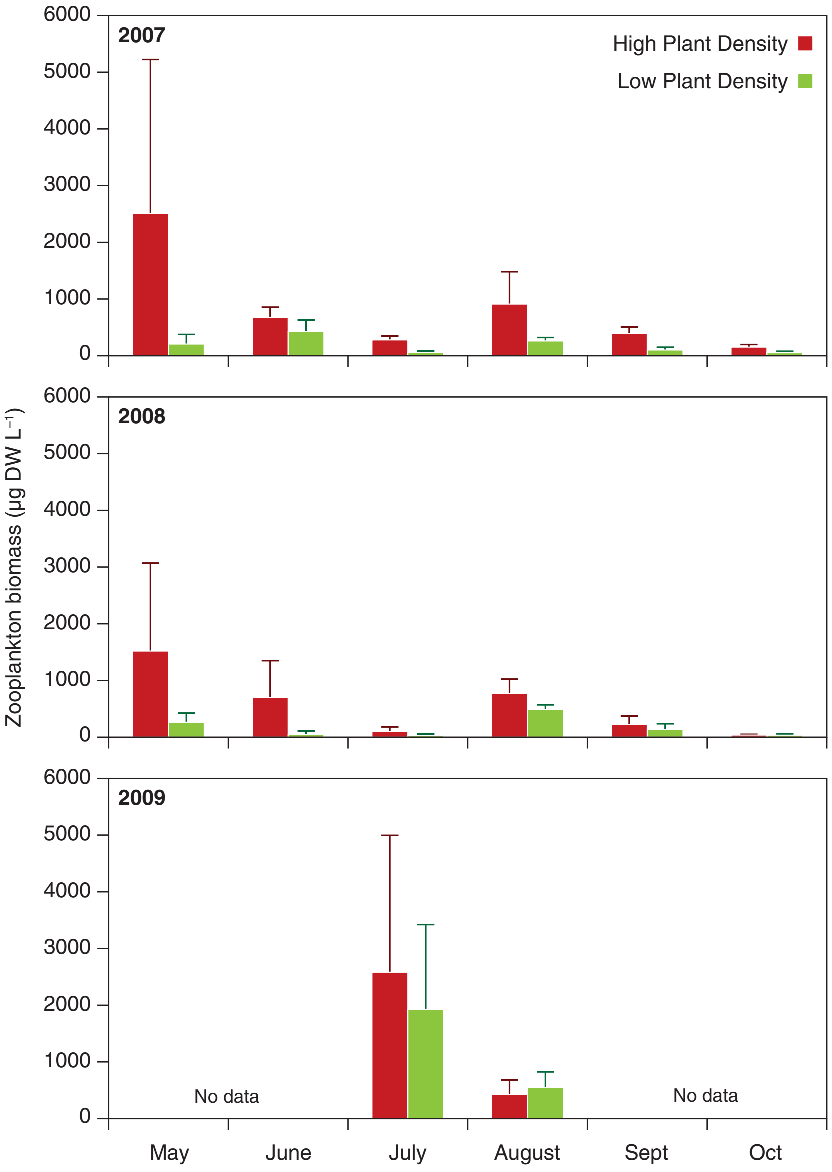
Figure 7. Perch (<15 cm) and roach caught in 6.25, 8 and 12.5 mm nets placed on the artificial plant beds in Lake Væng. Bars illustrate mean catch per net (1.5 m) ± S.D. (n=3). H and L refers to high and low plant density, respectively. (This figure is modified from Manuscript 2).



Perch were more abundant than roach in the artificial plant beds in Lake Væng (Fig. 7), and since perch are known to be more efficient than roach in feeding among submerged vegetation (Winfield 1986; Diehl 1988) it was assumed that only perch had a negative impact on macroinvertebrate densities. Even low plant volume infested (PVI) (>15-20 %) may reduce the predation effects of roach and three-spined sticklebacks (*Gasterosteus aculeatus* L.) on the zooplankton community if the fish are found in low numbers (Schriver *et al.* 1995). Our results on zooplankton biomass support the existence of some refuge effect at high plant density (Fig. 8). However, with the exception of Trichoptera in 2007, most macroinvertebrate groups did not exhibit higher densities in high plant density treatments. On the contrary, some taxa, such as Orthocladiinae, were more abundant at low plant density. It thus seems that other factors than refuge provided by high plant density affected the structure of macroinvertebrate communities.

Water turbidity and structural complexity of macrophytes are not the only factors impacting the interactions between invertebrates and their fish predators, also light levels can influence the hunting efficiency of fish (Diehl 1988; Miner and Stein 1993). Thus, floating-leaved macrophytes may provide a refuge for invertebrates by shading (Nurminen, Horppila, and Pekcan-Hekim 2007). When comparing macroinvertebrate densities on artificial free-floating and submerged plants we found a negative correlation between Secchi depth and the S/F-ratio (macroinvertebrates on submerged plants / macroinvertebrates on free-floating plants) in the Uruguayan lakes (Manuscript 3). Thus, when Secchi depth decreased the S/F ratio approached 1, meaning that differences in macroinvertebrate densities between the two plant types narrowed down. At high Secchi depth macroinvertebrate densities were relatively higher on the free-floating plants, indicating that these were a better refuge, potentially by shading the water below (Manuscript 3). In turbid lakes turbidity itself

Figure 8. Total biomass (µg DW L^{-1}) of zooplankton sampled from the artificial plant beds in Lake Væng. Error lines show ±1 S.D. Data are provided by D. Balayla (unpublished data).



provided a refuge for macroinvertebrates among both free-floating and submerged plants, thereby reducing the significance of shading. Fish are also expected to have a stronger impact on their prey in clear water lakes than in turbid lakes (Liboriussen *et al.* 2005; Radke and Gaupisch 2005; Pekcan-Hekim and Lappalainen 2006).

Fish biomass was also selected in the final model together with Secchi depth for explaining the S/F ratio in Uruguayan lakes (Manuscript 3). With increasing fish biomass differences in macroinvertebrate densities between the two plant types increased. However, since fish were more abundant among submerged than free-floating plants in Uruguayan lakes (Teixeira-de Mello *et al.* 2009), an increase in fish biomass would have had a stronger effect on macroinvertebrates among the submerged plants and thus have increased differences between plant types. The effect of plant type on macroinvertebrate density in our experiment (Manuscript 3) was also country-specific, since plant effects and S/F-ratio varied more in Danish lakes than in Uruguayan lakes. Most likely, this difference between countries was caused by the different fish communities, i.e. the refuge effect from free-floating plants was greater in Uruguayan lakes where fish densities were high (Teixeira-de Mello *et al.* 2009).

Cobb & Watzin (1998) found only moderate effects of fish predation on the prey community in a cage experiment in Lake Champlain although high fish density had a negative impact on chironomids and isopods. However, fish can alter the size structure of the macroinvertebrate community by feeding selectively on larger and more motile invertebrates (Crowder and Cooper 1982; Gilinsky 1984; Blumenshine, Lodge, and Hodgson 2000), and prey selection may furthermore be influenced by predator size and potential gape limitation (Huss, Byström, and Persson 2008). Perch undergo ontogenetic shifts as they grow – feeding to begin with on microcrustaceans, later on macroinvertebrates and eventually partly on fish (Allen 1935; Persson 1983b; Huss *et al.* 2008). These shifts and the inclusion of gradually increasing prey size in their diet are necessary for perch growth (Allen 1935). In Lake Væng small ostracods were less abundant during the first sampling round each year and overall lower in 2008 and 2009 compared to 2007, supposedly due to predation from the high number of perch in the frames (Fig. 7). We argue that perch later in the season fed to a larger extent on larger macroinvertebrates, potentially leading to a reduced predation pressure on ostracods (Manuscript 2). Such a shift is supported by our results on the microcrustacean community (Fig. 8) as microcrustacean biomass increased in August in both 2007 and 2008, indicating a declining predation pressure, possibly in consequence of an ontogenetic shift by the fish predator. The size when perch shift to macroinvertebrate feeding is highly variable, with an average of about 40 mm (Sandström and Karås 2002; Granqvist and Mattila 2004) or larger, (Hjelm, Persson, and Christensen 2000; Huss *et al.* 2008) and is affected by competition (Persson and Greenberg 1990a; Diehl 1993) and intraspecific interactions (Huss *et al.* 2008).

The apparently contradicting results of the impact of biomanipulation on benthic (Manuscript 1) and plant-associated (Manuscript 2) macroinvertebrates illustrate the importance of macrophytes. The densities of plant-associated macroinvertebrates found on the artificial plants were much higher than those found in the sediment, even when densities of YOY perch increase following biomanipulation and thus maintain a high predation pressure on the macroinvertebrates. Since macroinvertebrates are included in the diet of perch an increase in their densities may benefit the growth of small perch, which may eventually reach the piscivorous stage and thereby contribute to maintaining a clearwater state through predation on cyprinids. An enhance recruitment of perch to the piscivorous stage following expansion of submerged vegetation is supported by findings from the Swedish Lake Krankesjön (Hargeby *et al.* 2005) and seen in this light the establishment of submerged macrophytes following biomanipulation is crucial. However, in several lakes the expansion of macrophytes following biomanipulation has been delayed lakes (Jeppesen *et al.* 2005), possibly due to grazing by waterfowl (Søndergaard *et al.* 1996; Weisner, Strand, and Sandsten 1997; Marklund *et al.* 2002). Artificial plant beds, similar to those used in our experiment, have proved suitable as a daytime refuge for zooplankton (Schou *et al.* 2009), and since these artificial plant beds also increase the abundance of prey invertebrates available to perch and, with it, enhance their growth and potentially induce a shift to the piscivorous stage, establishment of artificial plant beds may be a useful tool to stabilise the clearwater state during the initial processes of lake recovery.

6.3 Plant-associated macroinvertebrates in a warmer climate

A temperature increase of about 0.2 ºC per decade during the next two decades is projected by the Intergovernmental Panel on Climate Change (IPCC) in several emissions scenarios, and best estimates for the temperature change by 2090-2099 relative to 1980-1999 range from 1.8 to 4.0 ºC depending on scenario (IPCC 2007). Such changes in temperature are expected to affect freshwater macroinvertebrate communities in various ways, such as timing of emergence (Elliott 1996; McKee and Atkinson 2000), distribution (Hickling *et al.* 2005), trophic interactions (Quinlan, Douglas, and Smol 2005) as well as community composition (Daufresne *et al.* 2004). Space for time substitution of experiments, where communities from different climate areas are compared, provides a good option for evaluating potential consequences of future climate changes, although other factors such as biogeographical differences and differences in lake age and thereby evolutionary history may be of importance as well. Interpreted with caution, comparisons of community composition and lake functioning between temperate and subtropical lakes (Meerhoff *et al.* 2007a; Meerhoff *et al.* 2007b; Teixeira-de Mello *et al.* 2009; Manuscript 3) can provide useful information on how temperate lakes will develop in a future warmer climate.

One of the most apparent differences between lakes in temperate and subtropical regions is those between fish communities in that subtropical lakes host much higher densities of small herbivorous or omnivorous fishes (Mazzeo *et al.* 2003; Teixeira-de Mello *et al.* 2009). Since fish may play a structuring role in macroinvertebrate communities (Crowder and Cooper 1982; Mittelbach 1988; Diehl 1992; Manuscript 1, 2) differences in macroinvertebrate communities were expected to appear in our comparisons of temperate and subtropical lakes. In agreement with this, both density, richness and diversity of macroinvertebrates were higher in Danish lakes than in Uruguayan lakes, likely due to the differences in fish communities between the two regions (Meerhoff *et al.* 2007a; Manuscript 3).

In temperate regions perch, and especially roach, may benefit from increased global warming and large cohorts of YOY can be expected (Lehtonen 1996; Graham and Harrod 2009). Consequently, a heavier predation pressure on macroinvertebrates in temperate lakes can be expected in the future. Following biomanipulation large year classes of fish may occur already today (Hansson *et al.* 1998), but in a future warmer climate fish densities may be even higher. Thus, in combination with clear water following lake shifts between alternative stable states fish are expected to have a strong negative impact on macroinvertebrate densities – as seen especially among the submerged plants in the Uruguayan clear water lakes (Manuscript 3).

In a future warmer climate macroinvertebrates may not only experience predation from fish but also competitive interaction. A positive effect of macroinvertebrate grazing on epiphyton (Cattaneo 1983; Brönmark 1989; Underwood *et al.* 1992) may be more likely to occur in cooler lakes compared to (sub)tropical lakes where fish to a larger extent are herbivorous or omnivorous (Winemiller 1990) and consequently may reduce the epiphyton biomass (Flecker 1992), and occupy niches that are occupied by macroinvertebrates in other regions (Wootton and Oemke 1992). In the Uruguayan lakes periphyton biomass was lower than in the Danish lakes but since also macroinvertebrate density was lower in the Uruguayan lakes (Fig. 5) macroinvertebrates were unlikely to be responsible for the reduced periphyton biomass. Large macroinvertebrates, such as freshwater shrimps (*Palaemonetes* sp.) and applesnails (*Pomacea* sp.), occurring only in the Uruguayan lakes (Manuscript 3), may feed on periphyton (e. g. Collins 1999; Carlsson and Brönmark 2006), resulting in reduced periphyton biomass. However, since no correlation was found between densities of large macroinvertebrates and periphyton biomass large macroinvertebrates were unlikely to have played a structuring role, and we therefore suggest that fish were the main controlling factor for periphyton biomass (Meerhoff *et al.* 2007a; Manuscript 3). Cyprinids, like roach and rudd (*Scardinius erythrophthalmus* Bonaparte), are likely to include more plant material in their diet under warmer conditions (Prejs 1984), and since cyprinid densities may benefit from a rise in a warmer climate (Graham and Harrod 2009) macroinvertebrates will face both competition for detritus and algae as well as predation from fish in the future.

The focus of lake restoration in temperate lakes has been directed at the shift between two alternative stable states – a clear water, macrophyte dominated state and a turbid phytoplankton dominated state (Scheffer *et al.* 1993); in warmer regions, however, dominance by free-floating macrophytes may form a *third* stable state (Scheffer *et al.* 2003). Areas dominated by free-floating macrophytes are likely to expand in consequence of warmer winters induced by the climate change. Our results show that a shift from dominance of submerged macrophytes to free-floating macrophytes will lead to lower densities of macroinvertebrates per square metre despite that free-floating macrophytes can serve as a refuge for macroinvertebrates when fish densities are high (Manuscript 3).

7 Concluding remarks and perspectives

The aim of lake restoration projects involving biomanipulation is to create a shift in lake trophic state (shift between alternative stable states c.f. Scheffer *et al.* 1993) from a turbid to a clear water state with dominance of submerged macrophytes. Here, I present results showing that both changes in fish community and in macrophyte coverage, as well as altered turbidity, have an impact on macroinvertebrate communities.

In accordance with *hypothesis 1* the density of benthic macroinvertebrates was found to increase shortly after a reduction in the stock of bream and roach. This increase was partly explained by a reduced biomass of fish and, with it, lower predation pressure on invertebrates and by the refuge effect provided by *E. canadensis*. Since plant-associated macroinvertebrate taxa appeared in the benthic samples during macrophyte years it was concluded that macrophytes also had a positive effect on macroinvertebrate density and richness. The proportional influence of each fish and macrophytes was, however, difficult to distinguish.

The bioturbation experiments showed that *Chironomus* larvae significantly increased the release of ammonium, SRP and total phophorous, as expected from *hypothesis 2*. Chironomids contributed largely to the peak in the density of benthic macroinvertebrates found 1990, and bioturbation-induced nutrient release was thus expected to increase after biomanipulation. However, high densities of benthic macroinvertebrates only occurred during the first years after the biomanipulation and, consequently, the effect on nutrient dynamics was expectedly short-term and most likely counteracted by increased nutrient retention caused by submerged macrophytes and benthic algae.

We found clear differences in $\delta^{13}C$ between invertebrates collected in years with and without macrophytes. Changes in CO_2 concentrations or in the flow of CO_2 from the sediment, induced by dense beds of *E. canadensis*, were most likely responsible for the increased $\delta^{13}C$ of phytoplankton and, consequently, the increased $\delta^{13}C$ of primary consumers and of organisms at higher trophic levels. These findings confirm the usefulness of stable isotope analysis of archived material (e.g. Sarakinos, Johnson, and Vander Zanden 2002; Feuchtmayr and Grey 2003; Syväranta *et al.* 2008) but also show their potential use in palaeolimnology where analyses of $\delta^{13}C$ of invertebrate remains can be used for studying past changes in lake trophic state.

In support of *hypothesis 3* we found artificial plant beds to support high densities of macroinvertebrates and there were strong indications that YOY perch were feeding on the macroinvertebrates and thus reducing densities. In the second year after the biomanipulation perch were larger in size compared to the previous years and they supposedly exerted a strong predation pressure on the macroinvertebrates despite lower perch densities. Furthermore, perch most probably benefitted from clearer water providing improved hunting conditions during this year.

The effect of turbidity on plant-associated macroinvertebrates was also evident when comparing macroinvertebrate communities between submerged and free-floating plants. The effect of turbidity on the distribution of macroinvertebrates may be of relevance in future warmer climate (IPCC 2007) where the risk of lakes being in the turbid state increases (Jeppesen *et* *al.* 2003; Jeppesen *et al.* 2009). In subtropical lakes, where the density of fish was high, free-floating plants harboured higher densities of macroinvertebrates than submerged plants, but as Secchi depth decreased differences between plant types became smaller. This illustrates well the refuge effect of free-floating plants (or their shade) in clear water and its substitution by the refuge created by turbidity in more eutrophied lakes. Despite that we found higher densities of macroinvertebrates per gram free-floating plant than per gram submerged plant, the density of macroinvertebrates per square metre will decrease if, in future, the third alternative state with dominance of free-floating plants (Scheffer *et al.* 2003) will prevail instead of submerged vegetation due to warmer winters.

In accordance with *hypothesis 4* densities of macroinvertebrates were also found to be lower in subtropical lakes than in temperate lakes, which was most likely due to the higher densities of small fish in the subtropical lakes. These herbivorous and omnivorous fish may both prey on and compete with the plant-associated macroinvertebrates; thus, since densities of small fish are expected to increase in temperate lakes due to global warming (Jeppesen *et al.* 2010) lower densities of plant-associated macroinvertebrates may be a likely future scenario.

Biomanipulation has proved to be an efficient tool for lake restoration. Often Chl *a*, total phosphorus, total nitrogen and suspended solids decreases as a result of the reduction in the zooplanktivorous and benthivorous fish stock and the often expanding coverage of submerged macrophytes (Søndergaard *et al.* 2008). Our results showed that reduced fish biomass and, especially, establishment of submerged macrophyte beds can lead to increased densities of macroinvertebrates. As an alternative to natural plant beds, whose establishment may be delayed, we found that artificial plant beds support high densities of macroinvertebrates. Macroinvertebrates, in turn, may serve as food item for perch, potentially enhancing its growth and facilitating its shift to the piscivorous stage. Consequently, artificial plants may accelerate the recovery processes of lakes following biomanipulation, an important role being further enhanced by their potential role as daytime refuge for zooplankton (Schou *et al.* 2009).

Thus it is suggested that the use of artificial plant beds is considered when planning future lake restoration projects. However it is also relevant to conduct further experiments for determining which size of plant bed and plant density that provides the best habitat for macroinvertebrates and at the same time serve as an optimal feeding ground for YOY perch. Since macroinvertebrates may form an important link in lake food webs (Vander Zanden and Vadeboncoeur 2002; Jones and Waldron 2003) studies of energy flow from macroinvertebrates to fish, especially to percids and cyprinids, would be relevant in future studies of lake recovery and restoration – not least when considering the potential changes in fish communities induced by climate change.

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1

CHANGES IN BENTHIC MACROINVERTEBRATE COMMUNITY AND LAKE ISOTOPE (C, N) SIGNALS FOLLOWING BIOMANIPULATION:

AN 18-YEAR STUDY IN SHALLOW LAKE VÆNG, DENMARK

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Manuscript

2

PLANT-ASSOCIATED MACROINVERTEBRATE RESPONSE TO BIOMANIPULATION: AN EXPERIMENT WITH ARTIFICIAL PLANT BEDS WITH CONTRASTING DENSITIES

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3

PLANT-ASSOCIATED MACROINVERTEBRATES IN TEMPERATE AND SUBTROPICAL SHALLOW LAKES ALONG TROPHIC AND FISH PREDATION GRADIENTS

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RESPONSE OF MACROINVERTEBRATES IN LAKES TO BIOMANIPULATION AND CLIMATE CHANGE

Effects of biomanipulation (i.e. removal of benthivorous and zooplanktivorous fish) on macroinvertebrates and their role in the recovering processes of shallow lakes were studied mainly in Danish Lake Væng. Density of benthic macroinvertebrates peaked two years after biomanipulation, coinciding with the establishment of submerged macrophytes and the reduced predation pressure from benthivorous bream and roach. During years with dense macrophytes $\delta^{13}C$ of invertebrates increased markedly, likely because the submerged macrophytes reduced the CO_2 concentration in the lake water and the flow of ^{13}C-depleted CO_2 from the sediment to the water phase, leading to higher $\delta^{13}C$ of phytoplankton and, consequently, of consumers. Analyses of $\delta^{13}C$ in remains of invertebrates in the sediment may therefore be a useful tool for identifying a shift from the clearwater macrophyte stage to the turbid phytoplankton stage in the past. Establishment of submerged macrophytes after biomanipulation can be delayed, but artificial plant beds may act as an alternative substrate and refuge for invertebrates in the initial recovery phase of lakes. During the second biomanipulation artificial plants positioned in the lake harboured high densities of macroinvertebrates. These may serve as prey for perch, allowing them to grow faster to the piscivores stage, where they can prey on cyprinids. However, lower densities of plant-associated macroinvertebrates found in subtropical lakes and a potential increase in fish densities in temperate lakes due to global warming indicate that we can expect a reduction in the abundance of plant-associated macroinvertebrates in a future warmer climate.

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