

# Fingerprints of planktivory - paleolimnological evidence of past fish community structure and dynamics

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Cover:subfossil of *Bosmina longispina*, photo by Emma Åhlén

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*To my beloved family*

# List of papers

This thesis is a summary of the following papers, which will be referred to by their roman numerals.

- I. Reinikainen, M. and Åhlén, E.  
**Viability of century old cladoceran ephippia: morphological variation in *Ceriodaphnia quadrangular* under historic changes in predation regimes**  
Submitted Manuscript.
  
- II. Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M.  
**Relationships between planktivore community capacity (PCC) and cladoceran microfossils in northern Swedish lakes**  
Fundamental and Applied Limnology **178**: 315–324.
  
- III. Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M.  
**Planktivore population dynamics affect body size characteristics of *Bosmina*: evidence from sediment archive and contemporary lake samples**  
Manuscript.
  
- IV. Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M.  
**Remains of *Bosmina* in sediments reflects historical changes in fish populations in a northern Swedish lake**  
Manuscript.

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# Abstract

Planktivorous fish affect the species composition, size and morphology of their zooplankton prey by size selective predation. Remains of cladocerans are deposited in the lake sediments and this microfossil community hence reflects the historical changes in the planktivore fish community. Most earlier work on quantitatively inferring past planktivory deals with ephippia (resting eggs) of *Daphnia*, however these remains are very scarce in northern Swedish lakes. In these lakes, often dominated by fish that are not obligate planktivores, such as perch (*Perca fluviatilis*), the individual size to a large degree determines the type of resource consumed. Therefore, in these lakes, the size distribution as well as the density of the fish community determines the overall planktivory

This thesis deals with evaluating the use of *Bosmina* remains in the sediment as indicators of past planktivory. I developed a transfer function based on *Bosmina* remains to be used in oligotrophic lakes with omnivorous species to reconstruct past planktivory. I test the transfer function in a lake where the history is to a large extent known. Furthermore, in this thesis a novel quantitative measure of planktivore pressure, the PCC (Planktivore Community Capacity) was developed. It was also possible to compare the morphology measurements of carapace length and mucro length of contemporary *Bosmina* sampled in the lake, with the same measurements on microfossils of *Bosmina* sedimented during the corresponding time period. By using the resurrection approach this thesis also evaluates the use of *Ceriodaphnia* clones as indicators of micro-evolutionary responses to past planktivory.

From the studies in this thesis I can draw some major conclusions; the morphological measurements carapace length and mucro length of *Bosmina* can be used to infer past planktivory in northern Swedish lakes. PCC has a higher explanatory power than CPUE in these lakes dominated by omnivorous fish. The morphology of the contemporary *Bosmina* corresponds well with the remains found in the sediment dating from the same time period. Both the contemporary and microfossil *Bosmina* changes in body size characteristics was in turn strongly related to PPC. Finally, the hatching of *Ceriodaphnia* ephippia is promising for studying past planktivory, both because of the high viability of the ephippia and the relationship between eye area and inferred PCC.

## Keywords

planktivory, foraging efficiency, cladoceran remains, *Bosmina*, planktivore community capacity, PCC, *Ceriodaphnia*, resurrection.

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# Introduction

In a long-term historical context, fish can be identified as a major resource for human populations. Evidence for the exploitation of this resource dates as far back as the mid-Upper Paleolithic period (Richards et al. 2001). In modern society, it is also evident that fish production and species composition are important factors both when it comes to commercial fishing and tourism. From an environmental point of view, fish populations have a marked effect on lake biological structure, affecting lake productivity, trophic status etc (Jeppesen et al. 1996 and references therein). Apart from exploitation of the fish resource, human activities like agricultural or domestic pollution have major effects on fish populations and food web structures (Jeppesen et al. 2001a). In this context human introductions (planned or accidental) of non-native fish species also can induce rapid shifts in lake conditions.

Not surprisingly, the reconstruction of former fish populations can be identified as a major conservation and management aim, with important implications for the understanding of lake food-web structure and underlying historical changes (Jeppesen et al. 2001a). From a reconstruction point-of-view, it is unfortunate that past fish populations cannot be directly derived from the paleological records that are formed in lake sediments. However, since the trophic dynamics in lake ecosystems are affected by the composition of fish populations, there are other data that can be used to infer past fish population structure. Such methods (reviewed by Jeppesen et al. 2001b) rely on known effects of fish populations on lower trophic levels, which can be recorded from microfossils in lake sediments. Ultimately, these signals can be used to quantitatively reconstruct fish populations, using so-called transfer functions (Jeppesen et al. 2001b). Transfer functions were originally developed to infer pH from diatoms in sediments (see e.g. Birks et al. 1990), and have later been applied to study a number of other relationships, including long-term climatological changes (see Rosén et al. 2001 for recent examples).

However, the understanding of relationships between predation pressure and microfossil data is mainly qualitative (Jeppesen et al. 2001b), and so far only few examples exist of quantitative reconstructions of past fish populations from sediment microfossils (Jeppesen et al. 1996, Jeppesen et al. 2002, Amsinck et al. 2006). Future reconstruction work in different geographic regions also requires a profound analysis of alternative microfossil – predator relations (Jeppesen et al. 2001b). Different predators have highly variable impacts on invertebrate communities and certain fish

species feed predominantly on zooplankton only as young, whereas most of the earlier work on predator – microfossil relations has included planktivorous fish only. Furthermore, invertebrate predators (which dominate under heavy piscivory or in the absence of fish) may drive zooplankton towards larger body sizes, whereas planktivory by fish typically change the zooplankton community to smaller body sizes.

## **Planktivory**

It is well established that planktivorous fish affect the species composition and size distribution of zooplankton in lakes through either size specific predation, or indirectly through trophic interactions (Brooks and Dodson 1965, Kerfoot 1974, Ives 1999). High planktivory in a lake generally shifts the zooplankton community towards species of smaller body size and smaller body size within species. Most fish are visual predators and preferentially select the largest zooplankton prey (Brooks and Dodson 1965). Cladocerans are often preferred prey because they have a conspicuous way of moving (Zaret 1980). Experimental manipulations of fish density (Post and McQueen 1987), fish introductions into previously fishless lakes (Donald et al. 2001, McNaught et al. 1999) and introductions of new/alien zooplanktivorous fish (Amundsen et al. 2009, Berg et al. 1994) all show similar changes in the zooplankton community, i.e. an increase in planktivory led to smaller sized zooplankton and/or decreased planktivory led to larger sized zooplankton.

It can be complicated to quantitatively describe or calculate the effects of fish predation on the zooplankton community since fish of different species and size (age) affect the zooplankton community differently (Figure 1). Still, in species that are obligate planktivores the effect of planktivory is rather direct and straightforward to measure as all individuals feed on zooplankton. For species that are not obligate planktivores, the size and age of each individual is much more important. For species that undergo an ontogenetic niche shift, the diet alters as the fish grows. Perch (*Perca fluviatilis*) and Arctic char (*Salvelinus alpinus*) are examples of fish that change diets from being planktivorous to eating macroinvertebrates to end up as piscivores (Persson 1988, Byström 2006). On top of this these species are cannibals feeding on their own, mainly planktivorous, young. Hence, in systems dominated by species that undergo ontogenetic niche shifts planktivory pressure may vary substantially, dependent on the size structure of the population. For example, if there is a dominance of young of the year (YOY) and one year old individuals, the planktivory pressure is high, whereas if larger individuals



dominate the system the degree of planktivory is low (e.g. Persson et al. 2004, Byström 2006).

### **Invertebrate remains in sediments**

When organisms die, their remains may end up as microfossils in the sediment. The most important factor affecting the preservation in sediments is the chemical composition of different body parts (Korhola and Rautio 2001). After death and also after moulting zooplankton disarticulate into different parts of their exoskeleton, such as carapaces, headshields, mandibles, antennas, claws and post-abdomens (Korhola and Rautio 2001).

Zooplankton in lakes can be divided into two main groups, Cladocera and Copepoda, which are both small crustaceans and important as a food resource for fish (Northcote 1988). There are also other groups/taxa that are part of the zooplankton community and also eaten by fish such as the Anostracan fairy shrimps and the Dipteran phantom midges (*Chaoborus*).

Copepod body parts are not at all preserved in the sediment. Their exoskeleton is too soft and fragile, and despite the great abundance of copepods in the water column their body parts are totally absent from the sediment archive (Korhola and Rautio 2001). Anostraca, fairy shrimps are well known to not be able to coexist with fish because they are large, visible and slow moving and hence very sensitive to fish predation (Näslund et al. 2002). Fairy shrimps should therefore be an excellent indicator of fish introductions into fishless lakes as when fish are introduced the fairy shrimp go extinct (Nilsson 1972). In a pilot study, we found that the mandibles of *Polyartemia forcipata* are well preserved in the sediment (Åhlén unpublished data). Similarly, *Chaoborus* spp., phantom midge larvae can be used as an indicator of absence of fish, most species have an anti predator behavior with vertical migration and are almost invisible, enabling them to coexist with fish (Borkent 1981). There are, however, a few species that lack this behavior and that are also more pigmented, such as *C. americanus* and *C. obscuripes* (Stenson 1981, Berendonk and Bonsall 2002). Such species have been shown to disappear from lakes when fish are introduced (Northcote et al. 1978) and invade after fish extinctions (Lamontagne and Schindler 1994). Remains of *Chaoborus* mandibles found in the sediment have been used to detect fish absence or presence (Uutala 1990, Sweetman and Smol 2006) and also to detect historical changes in fish communities (Palm and Svensson 2010). Palm et al. (2011) showed that fragmentation of *Chaoborus* mandibles can indicate cyprinid fish. First they showed that

roach (*Rutilus rutilus*), a cyprinid fish fed *Chaoborus* larvae in an aquaria experiment evacuated a significantly higher degree of fragmentation of the *Chaoborus* mandibles than perch (*Perca fluviatilis*). They compared the remains of *Chaoborus* mandibles from surface sediments of lakes with and without roach and found also there a higher degree of fragmentation in the surface sediment from the lakes containing roach. In a paleolimnological study, they also found a higher degree of fragmentation of the *Chaoborus* mandibles from the sediment layers during a period when the lake had contained roach comparing to when roach had disappeared (Palm et al. 2011).

Cladoceran remains are the dominant microfossils in sediments due to their chitinous exoskeleton (Korhola and Rautio 2001). Several structures of the cladocera exoskeleton are preserved in the sediment, such as the headshields, carapaces and post-abdomens (Korhola and Rautio 2001). However, there are also some species of cladocerans that are not represented at all in the sediment archive (e.g. *Poluphemus pediculus*, *Scapholeberis mucronata* and *Diaphanosoma brachyurum*, Davidson et al. 2007). The degree of preservation of the cladocera remains differs a lot among the genera. For *Daphnia* for example only the post- abdomens and ephippia (resting eggs) are found in the sediment in good shape, whereas for *Bosmina* and many of the species associated to vegetation and the littoral zone such as Chydoridae the head shields and carapaces are well preserved (Korhola and Rautio 2001).

Much work has been done using remains of cladocerans as indicators of different ecological and environmental changes during a lake's history. Some examples are: acidification/ pH (Sarmaja-Korjonen 2002), trophic state/eutrophication (Brodersen et al. 1998), temperature (Duigan and Birks 2000, Lotter et al. 2000), salinity (Bos et al. 1999), lake depth/level (Bos et al. 1999, Korhola et al. 2000, Sarmaja-Korjonen 2001), forestry (Bredesen et al. 2002) and macrophyte density (Davidson et al. 2010). Remains of cladocerans have also been used qualitatively to show historical effects of planktivory. The shift in dominance of larger to smaller zooplankton species due to planktivory has not only been observed in contemporary sampling but is also well documented in the sediment (Kitchell and Kitchell 1980, Leavitt et al. 1989). Similarly, reduced size within species has been documented in sediment archives (Warshaw 1972, Salo et al. 1989).

The ephippia of cladocera are also preserved in the sediment and form an "egg bank". These eggs can be viable for a long time and hatch when exposed to the right environmental conditions (Brendonck and De Meester 2003). For instance, *Daphnia* ephippia may be viable for more than one century

(Caceres 1998, Michels et al. 2007), although a few decades appears more typical (Brendonck and De Meester 2003).

Resting eggs or ephippia can be hatched in the laboratory enabling studies of ecological changes over time periods that would be impossible using observations on contemporary populations; this approach is often referred to as resurrection ecology (Kerfoot et al. 1999). Zooplankton hatched from resting eggs have successfully been used to study changes in life-history, behavioral, or genetic characteristics in response to varying selective forces (reviewed by Brendonck and De Meester 2003). An advantage with cladocerans in experimental work is that they form parthenogenetic clones. *Daphnia* clones have been used in several evolutionary studies, such as investigations showing adaptation in resistance to pollution (Kerfoot et al. 1999) and cyanobacteria toxins (Hairston et al. 1999). More recently *Daphnia* has been used to understand fitness consequences of hatching and reproduction success (Brede et al. 2007), to study changes in the strength of interspecific competition (Steiner et al. 2007), and to study the microevolution of diel vertical migration (Michels et al. 2007).

### **Inferring past planktivory**

In order to use remains of invertebrates or other organisms to reconstruct historical changes in lakes, the development of a so called transfer function is essential (Jeppesen et al. 2001b). The first step is to develop a surface sediment calibration (or training) set, consisting of surface sediment samples of a variety of lakes, combined with the corresponding contemporary data on environmental variables, such as area, depth, water chemistry, temperature and fish density. The surface sediment samples are processed and the biological remains of interest – in this case Cladocera – are analyzed. Multivariate statistical techniques are used to analyze which of the measured lake variables are important influencing the Cladocera community. The relationship between a specific variable and species distribution or morphological measurements is quantified in the form of a transfer function.

Fish communities have also been quantitatively reconstructed using remains of cladocerans from lake sediments (Jeppesen et al. 1996, Jeppesen et al. 2002, Amsinck et al. 2006). Much of this work has focused on the size of resting eggs, ephippia from *Daphnia*; these have been used to develop transfer functions to reconstruct past fish predation (Jeppesen et al. 2000, Jeppesen et al. 2002, Jeppesen et al. 2003). However *Daphnia* have proved

to be rare in our study area, i.e. oligotrophic northern Swedish lakes (Wahlström et al. 2000, Byström et al. 2004). Since *Daphnia* are scarce we focused on a different genus of cladocera, i.e. *Bosmina*. The preservation of *Bosmina* in the sediment is high because it has a chitinous exoskeleton and is thick-bodied, and therefore gives a relevant reflection of the population of the water column (Amoros and Jaquet 1987, Nykänen *et al.* 2009). Moreover, studies have shown that body size, the length and shape of the antennules and the length of the mucro differ depending on the predation regime that dominates in the lake (Kerfoot 1975 and 1977, Nilssen and Sandøy 1990, Sweetman and Finney 2003). When planktivorous fish are abundant the body size of *Bosmina* tends to be small and antennules and mucros are short, whereas the body size is overall larger with longer antennules and mucros when planktivorous fish are rare or absent (Kerfoot 1981, Johnsen and Raddum 1987). The lengths of antennules and mucros have been used to reconstruct the history of planktivorous fish predation (Kerfoot 1981, Kitchell and Carpenter 1987). Thus, *Bosmina* should be an excellent species for constructions of transfer functions for the reconstructing of past planktivory pressure and hence fish community composition in northern oligotrophic lakes.

Earlier quantitative studies of past planktivory reconstructed from microfossils of cladocera have used catch per unit effort (CPUE) as measurement of planktivory (Jeppesen et al. 1996, Jeppesen et al. 2002, Amsinck et al. 2006). Both catch per unit effort in number (CPUE<sub>n</sub>) and weight (CPUE<sub>w</sub>) have been successfully employed on large data sets that include different combinations of lakes from Denmark, New Zealand, and Greenland (Jeppesen et al. 2000, 2002, 2003). These earlier studies show that especially when the fish stock is dominated by obligate planktivores (e.g. in eutrophic and turbid lakes; Persson et al. 1988), significant correlations between CPUE and cladoceran microfossils can be obtained. However, oligotrophic or dystrophic lakes, which are common in northern Europe, are often dominated by fish species that are not obligate planktivores, like perch (*Perca fluviatilis*) and Arctic char (*Salvelinus alpinus*). These species undergo ontogenetic niche shifts and as they grow, they shift diets from zooplankton to macroinvertebrates and finally end up as piscivores (Persson 1988, Byström 2006). When the fish community is dominated by such ontogenetic omnivorous species, the number or weight alone in CPUE measures does not necessary give an accurate estimate of the degree of planktivory in a lake.

# Objectives

Cladocera sub-fossils have been successfully used to quantitatively infer past planktivory in lakes dominated by obligate planktivores, mainly focusing on ephippia from *Daphnia* (Jeppesen et al. 1996, Jeppesen et al. 2002, Amsinck et al. 2006). However, the northern Swedish lakes studied here have a fish fauna that is typically dominated by perch or Arctic char, which are not obligate planktivores. Moreover, remains from *Daphnia* in the sediment have proved to be very scarce. Therefore the main objectives in this thesis were to:

1. Evaluate the use of *Bosmina* remains in sediments as indicators of past planktivory
2. By using the resurrection approach evaluate the use of *Ceriodaphnia* clones as indicators micro-evolutionary responses to past planktivory.
3. Develop and test a quantitative measure of planktivory pressure for fish communities dominated by omnivorous fish species.
4. Develop transfer function based on *Bosmina* remains to be used in oligotrophic lakes with omnivorous species to reconstruct past fish communities

# Approaches and methods

## Planktivore capacity

Since fish communities in oligotrophic or dystrophic lakes are to a large extent dominated by species which are not obligatory planktivorous, we developed a new way of measuring planktivory based on the size- and species specific attack-rate of each individual fish caught (Figure 1). This mechanistic approach to estimate and describe potential impact of an individual fish on zooplankton is based on laboratory estimates of size

dependent capture rates on zooplankton (Wahlström et al. 2000, Hjelm and Persson 2001, Byström and Andersson 2005). In short, the higher the attack rate an individual has the more efficient it is as planktivore.

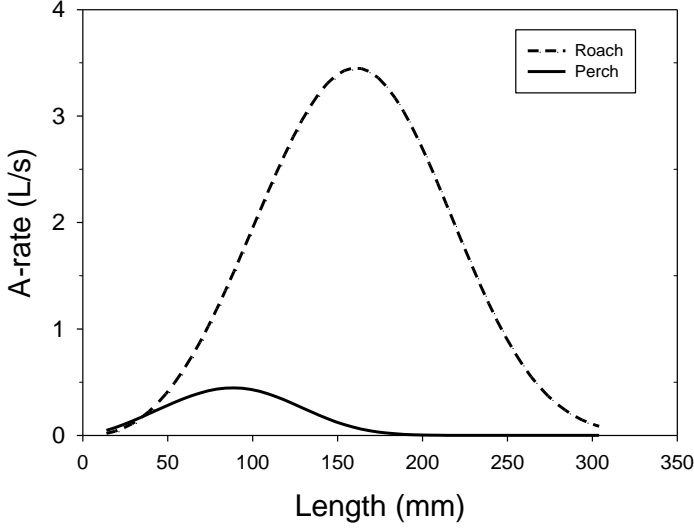


Figure 1. Size dependent attack rates of perch and roach on a 1 mm *Daphnia* (redrawn from Hjelm and Persson 2001 and Wahlström et al. 2000), illustrating the difference in attack rate between an obligate planktivore (roach) and an omnivore the undergoes ontogenetic niche shifts (perch).

We sampled the fish community with the same methods as Jeppesen et al. (1996), Jeppesen et al. (2002), and Amsinck et al. (2006). We used standardized multiple mesh size gill nets (Nordic nets, 1.5m deep with 12 different 2.5 m long sections with mesh size from 5 to 55 mm, Appelberg 2000). To obtain a quantitative measure of zooplankton predation pressure in the lakes we estimated the attack rate on zooplankton for each individual fish caught in the gill nets according to equation (1).

$$a(w) = A \left( \frac{w}{w_{opt}} \exp \left( 1 - \frac{w}{w_{opt}} \right) \right)^\alpha \quad (1)$$

Where  $a(w)$  is the attack rate at fish weight  $w$ ,  $A$  is the maximum attack rate,  $w_{opt}$  is fish weight at the maximum attack rate, and  $\alpha$  is a size scaling-exponent. Species specific parameter values of  $A$ ,  $w_{opt}$  and  $\alpha$  were then obtained from the literature. We thereafter used these estimates to obtain an estimate of total zooplankton predation pressure which we entitle Planktivore Community Capacity (PCC). PCC was obtained by summing the attack rates for each individual fish and dividing the sum of the attack rates of all fish by number of gill nets. In this way, a fish community attack rate per unit effort was obtained. We also developed a direct quantitative measure of planktivore efficiency that was based on absolute estimates of densities and size structure of the perch population in a lake obtained from marc-recapture methods. Since this measure is an estimate of the total fish population attack rate on zooplankton we chose to call it the Planktivore Population Capacity. The PPC differs from the PCC by being an absolute measure, rather than a relative measure as the PCC is. We use the PPC in paper III and IV where we used data from only one lake, lake Abbortjärn 3, in which the fish population has been studied and described in detail.

### **Cladocera remains and *Bosmina* morphology**

The subfossil cladocera analysis was conducted by heating approximately 5 g wet sediment in 25 ml 10 % KOH for 30–60 minutes before passing through a 100  $\mu\text{m}$  sieve. From each sample, microfossils were counted until at least 100 of the most abundant remains had been counted from a known volume, i.e. 5–100 ml depending on density. When developing the transfer function (paper II); the head shields, carapaces and ephippia from *Bosmina* spp. were counted from each sample. The headshields were identified to species level, and we identified two species of *Bosmina* present in the sediments, *Bosmina longispina* and *Bosmina longirostris*. Ephippia from *Ceriodaphnia* spp. and head shields and carapaces from chydorid species were also counted; none of these were identified to species level. The following measurements were taken from *Bosmina*: carapace length (CL), mucro length (ML), antennule length from the “tooth” to the tip (AL) and height of the antennules (H) (see Fig. 2). The number of antennule segments were also counted from the tooth to the tip. The measurements from the headshields (AL, L, H and number of antennule segments) were all from *Bosmina longispina*. For these morphological measurements 20 carapaces were measured and 20 head shields from each sample. In the following studies (papers III, IV and I) we focused only on carapace length and mucro length on *Bosmina*.

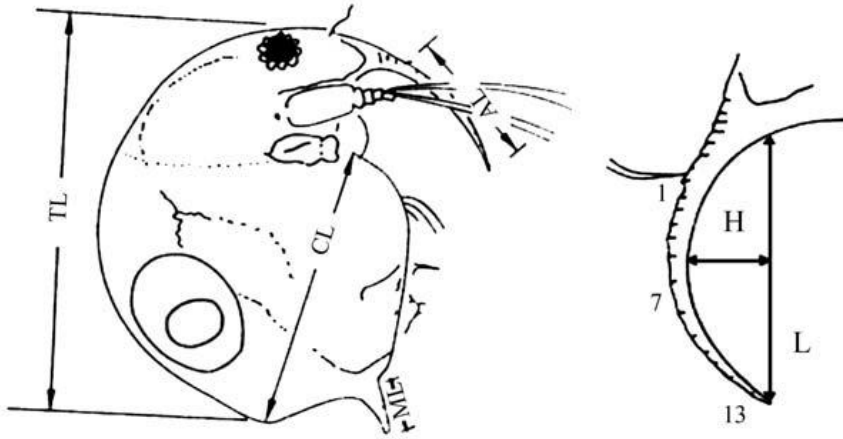


Figure 2. Morphological measurements on *Bosmina*, modified from Kerfoot (1975). Where CL = carapace length, ML = mucro length, AL = antennule length and H = height of the antennule.

### **Sediment sampling and sediment dating**

Lake sediments accumulate constantly; this process starts as soon as the lake is formed. The sediment consists of both autochthonous matter (produced within the lake), and allochthonous material (from the surrounding catchment and atmosphere). Everything that is produced within the lake (and distributed to it) is sedimented onto already existing sediment creating an environmental archive with progressively younger sediment towards the sediment surface (Smol 1992).

There are several different techniques for sediment sampling (Glew et al. 2001), we have used two of them; the HTH-gravity corer (Renberg and Hansson 2008) and the freeze core (Renberg 1981), all sampling was done in the deepest part of the lake, where sediment accumulates. The HTH-gravity corer is used to collect fresh sediment and was used in paper I, where it was important for the viability of the ephippia that the sediment was not frozen and in paper II, where we only used the surface sediment (the uppermost centimeter).



The freeze corer was used in paper III and IV where the technique of the sediment freezing onto the corer enabled us to collect sediment with minimum amount of disturbing, important for the dating. The sediment in Lake Abbortjärn 3 (paper I, III and IV) is not varved on a yearly basis but does have a laminated structure indicating a low degree of mixing due to bioturbation. To establish an adequate sediment chronology, we used a dating technique based on radio-isotopic Pb-210, with a half life of 22.3 years, which is useful for sediment ages of up to 150 years (Appleby 2001). One side of the core was divided into three longitudinal sections; one section was used for <sup>210</sup>Pb-dating and the other two for cladoceran analysis. The section that was used for dating was sliced into 1 cm thick samples starting from the sediment surface, freeze dried and analyzed for <sup>210</sup>Pb-activity. The remaining two sections (1 cm wide) were sliced into 0.5 cm thick samples to provide a sufficient amount of sediment material for analyzing cladoceran remains (ca 5 g wet weight). To further increase the time resolution, e.g., to be able to detect changes in cladoceran remains with greater stratigraphic resolution, the two sections were sliced with a 0.25cm overlap. Hence one section started from the sediment surface (i.e., 0-0.5 cm, 0.5-1 cm, etc) until 13 cm below the sediment surface, while the other section started from 0.25 cm below the sediment surface (i.e., 0.25-0.75 cm, 0.75-1.25 cm, etc) until 13.25 cm below the sediment surface.

# Summary of results from papers I-IV

## I

The objective of this paper was, partly to explore the hatching of cladocerans in relation to inferred sediment age, and also to more specifically study the hatching and characteristics of *Ceriodaphnia* in relation to inferred sediment age and lake dynamics.

We collected fresh sediment that was sliced in 0.5 cm slices from 0-15 cm of sediment depth. The inferred sediment date from these samples was established by analyzing remains of *Bosmina*. We used the morphological character mucro length from the *Bosmina* remains to achieve an indirect dating based on a Pb210-dated core, taken within the same lake-basin.

The sediment samples were put in separate jars in a climate chamber and checked weekly. Apart from counting all individuals from each species and sediment depth we took out a maximum of 15 individuals of *Ceriodaphnia* and transferred them individually to culture bottles to rear clones. We measured mucro, carapace, neck-spine and eye-area from both clones and individuals preserved directly after hatching. The *Bosmina* morphology profile corresponded very well with the profile from the Pb210-dated core, which made it possible to use this as an indirect dating method by aligning the two curves. The relationship between fish predation intensity and *Bosmina* microfossil morphology that earlier has been established from the dated core (paper IV) was also present in the profile from the fresh sediment core; correlations between the cores were highly significant (Pearson's  $r$  for mucro-and carapace-lengths were 0.89 and 0.86 respectively;  $p < 0.001$  in both cases).

The hatching profile obtained showed that there were numerous viable resting eggs in the uppermost layers of the sediment from *Bosmina*, *Ceriodaphnia* and *Holopedium*. Deeper down, at 3-3.5 cm sediment depth i.e. an inferred sediment age of 15 years, the number of hatchlings from *Holopedium* and *Bosmina* started to tail off. *Ceriodaphnia* was found to hatch in large numbers down to ca 20 years (5 cm depth), and also hatched more frequently even deeper down. The maximum inferred sediment age for ephippia to still be viable was ca 115 years (15 cm depth) for *Ceriodaphnia*, ca 70 years (13 cm depth) for *Holopedium*, and ca 45 years (9.5 cm sediment depth) for *Bosmina*.

For the *Ceriodaphnia* individuals preserved directly upon hatching there was a significant difference between sediment layers regarding eye-area, which was smallest in individuals from the 2-2.5 cm sediment layers; individuals in the uppermost layer had the largest eye-area. For mucro there was not such an effect. In this newly hatched generation a neck-spine was present in 74% of the individuals. The neck-spine height differed significantly between the sediment layers, but no distinct trends in relation to changes in fish predation could be identified.

None of the morphological characters measured from the isolated and laboratory grown *Ceriodaphnia* clones showed any significant difference between the sediment depths (ANCOVA) Neck spines were only present in 10.2% of these animals and were therefore to scarce to be statistically analyzed.

In this study the most promising species for isolating clones from the egg bank was *Ceriodaphnia quadrangula*. Even though both *Bosmina* and *Holopedium* had viable eggs as old as 45 and 70 years respectively, the *Ceriodaphnia* ephippia were viable at ages up to 115 years, suggesting that *Ceriodaphnia*-ephippia may survive at least as long as *Daphnia* (Michels et al. 2007, Caceres 1998). Apart from that we found a morphological trait, the eye-area, which corresponded well with changes in predation regime. The eye-area was smallest around the inferred peak in fish predation, being 50 % smaller than the average of the other exephippial clones. A conspicuous character on prey like the compound eye is an important cue for visually oriented planktivorous fish (Branstrator and Holl 2000). However, the compound eye is of vital importance in cladocerans for phototaxis (e.g. diel vertical migration) and orientation of the body axis during swimming movements (Ringelberg 1999). Thus, a trade-off between optimal eye-size for swimming behavior and visibility to predators seems likely. Our results suggest that fish predation may select for smaller eye-size.

We could not, however, show a genetic response to intensity in fish predation through the decrease in eye-area following high fish predation in laboratory grown clones.

Hence, the animals preserved upon hatching, representing the first exephippial population differed, from the laboratory population in two ways. Firstly, they showed variation in eye-area, and secondly they typically had conspicuous neck-spines. These differences among the two populations suggest phenotypic plasticity in eye-size and neck-spine production.

## II

In this paper we wanted to develop a calibration data set of surface sediment cladocera remains correlated with planktivore predation pressure in 39 northern Swedish lakes.

We chose to study how the species composition of the cladoceran remains was altered due to planktivory by choosing three different ratios; the proportion of *Bosmina longispina* to *Bosmina longirostris*, the proportion of chydorid species to *Bosmina* spp. and the proportion of *Ceriodaphnia* spp. to *Bosmina* spp. We also chose to focus on the morphology of *Bosmina*. The different morphological characters of *Bosmina* that we measured were the number of antennula segments, the height of the antennules, the size of the carapace and the mucron length.

In this paper we propose a novel way of estimating planktivory in lakes, planktivore community capacity (PCC). PCC takes into account the size and species specific foraging efficiencies of fish on zooplankton, which is important in lakes not dominated by obligate planktivorous fish.

We show here that PCC has a higher explanatory power than CPUEn in these lakes, which are not dominated by obligate planktivores. We believe this is because PCC considers potential planktivory impact by fish of specific sizes and species that CPUEn and CPUeW ignores. The relationship between PCC and CPUEn is strongest in the group of lakes where the ratio PCC:CPUEn  $> 1$ . In these lakes more than 30% of the fish caught were obligate planktivores (roach or bleak). These lakes can be compared to lakes described in earlier studies (Jeppesen et al. 2000, Jeppesen et al. 2002), where CPUEn has proven to be a satisfactory estimate for planktivory and directly usable to establish relationships between fish predation and palaeolimnological indicators. In contrast, lakes with a high CPUEn, a low PCC and PCC:CPUEn  $< 1$  appeared to have a weaker relationship between these variables. These lakes are dominated by perch or by Arctic char in the mountain lakes.

Our results show that remains of *Bosmina* are an effective indicator of planktivore pressure, both regarding species composition and morphological traits. PCC was negatively correlated with the proportion of *Bosmina longispina*, i.e. with higher predation pressure *Bosmina longirostris* becomes relatively more important. *Bosmina longirostris* is an indicator of eutrophication and typically becomes more abundant with increased trophic status (Stenson 1976, Gašiorowski and Szeroczyńska 2004). Regarding morphology, our results show that carapace length was negatively correlated to PCC. Since we cannot determine from the carapace alone which species of

*Bosmina* the carapace belongs to this change can be caused both by an increasing proportion of *Bosmina longirostris*, as our results suggest, and also by a change towards smaller individuals of both species with increasing PCC. Our results also show that mucro length is negatively correlated to PCC. Since the mucro is mainly a defence towards invertebrate predators this is in line with the commonly observed pattern of decreasing pelagic invertebrate predators with increasing vertebrate planktivore densities (Kerfoot 1981).

We suggest that the use of PCC in combination with sediment remains of *Bosmina* is a powerful approach to estimate past planktivore predation pressure, and that this approach will produce more accurate correlations to different response variables of planktivory effects compared to prior methodology. This relates to the fact that PCC estimates are based on the independent planktivory efficiency measurements of individual fish, thus documenting a specific impact on zooplankton, which depends on the fish community present in the lakes.

### III

In this study we take advantage of a high resolution long term study on the population dynamics of perch in Abbotjärn 3 during 1992-2000. We here have information regarding the temporal variation in density and size structure of perch and hence variation in planktivory pressure on zooplankton. We studied the effects of these variations on *Bosmina* body size characteristics in both contemporary zooplankton samples in lake water and in corresponding microfossil remains in lake sediment.

As we used estimated population densities instead of CPUE effort data to estimate the temporal variation in overall planktivory pressure on zooplankton we define the measure of predation pressure as Planktivore Population Capacity, PPC instead of PCC which is based on relative CPUE data.

We measured the body size characteristics mucro length and carapace length on *Bosmina* spp. both from the lake water and from the microfossil remains in the sediment to study whether these measurements from the microfossils reflect corresponding measurements on ambient zooplankton from the lake. We also tested if the variations in body size characteristics in *Bosmina* microfossil remains and in lake water correlate with our estimates of planktivory in the lake (PPC).

The PPC varied substantially over the study period, being low in the beginning of the study period (1992-1993) and in the end of the period (1999-2000) and high during the period 1994-1998. The carapace and mucro length for both contemporary and sediment *Bosmina* showed the opposite pattern and were largest during the periods when the PPC value was low and with smaller sizes during the middle period when PPC was high. Correspondingly, negative correlations were present in both lake water column samples and sediments for both carapace and mucro size and PPC. Both carapace and mucro length from the contemporary zooplankton samples from the water column correlated well temporally with those from the sediment samples (carapace length,  $r = 0.89$ ,  $p < 0.01$  and mucro length,  $r = 0.90$ ,  $p < 0.01$ ).

The densities of perch were divided into three age classes, YOY, 1-year old and  $\geq 2$  years old. Overall, small perch contributed most to PPC, more than 80% in all years except for 1996 and 1999 when the 1-y old perch contributed with more than 50% to PPC.

The size measurements on microfossils of *Bosmina* in the sediment showed strong temporal correlations with contemporary measurements on *Bosmina* from the water column in our study lake. This strongly suggests that we were able to get a high resolution of our measured microfossils from the dated sediment and that these were well preserved in the sediment. The sizes of carapace and mucro were however never as small in the sediment data as in the corresponding samples from the contemporary data during the period of high PPC. This is not surprising since the samples from the water column are only collected during the period of most intensive planktivory, whereas the sediment data represents the accumulation of remains over a longer period. Nevertheless we find a strong correlation between the microfossil remains from the sediment and the contemporary zooplankton samples from mid to late summer 1993-2000, suggesting that body size characteristics of *Bosmina* can be used to accurately reconstruct past changes in the same characteristics of *Bosmina* in the lake. Thus, this study proved that the major advantage of sedimentary data, i.e. data that can be collected at a single occasion including information of a very long time period, can be used as a powerful tool to prolong time series derived from long-term limnological data.

We found that YOY perch accounted for more than 80% of the PPC, regardless of whether the PPC was high or low. When studying fish populations effects on zooplankton communities YOY fish are most often not accounted for because they are simply not caught by standard approaches such as multimesh gillnet sampling. Our approach with calculation of PPC

has shown the importance of these small size classes for planktivory intensity, especially in lakes dominated by not obligate planktivores.

#### IV

In this study we applied our transfer function for Planktivore Community Capacity, PCC (from Åhlén 2011) on remains of *Bosmina* in the sediment from a lake where parts of the history is known. This was done to evaluate whether we are able to detect historically documented changes in the planktivore pressure, and to provide quantitative estimates of past fish predation. We used the morphological measurements of carapace length and mucro length from *Bosmina* remains in the sediment to reconstruct PCC for a more than 60 year long period. The sediment was extracted from a core dated with Pb-210. The history of the fish population in the lake is known on a descriptive level since 1957; in recent years, since 1992 it has been extremely well studied.

The values of PCC were first, from the 1940ies to the mid 1960ies high; thereafter they gradually decreased until 1990. During the period 1992 to 2000 there was first a dramatic increase and thereafter a dramatic decrease in PCC to low levels in 2000. These shifts correspond well to the history that is known about the fish community in the lake. According to an inventory conducted in 1957 there was perch and nine spined stickleback in the lake. These two species are known not to coexist for long periods since perch prey on stickleback and eventually exterminates them in small lakes (Englund et al. 2009). Since there are sticklebacks in several neighboring seepage lakes we conclude that the lake most probably was inhabited by nine spined stickleback before the 1957 inventory. This correlates well to the high PCC level; sticklebacks are efficient zooplanktivores when alone in small lakes (Johansson and Wahlström 2002, Byström et al. 2007). According to local fishermen, and recommended by the 1957 inventory, the lake was stocked with brook trout in the early 1960ies. This introduction was however not successful. Perch has been present in the lake ever since before 1957, but we do not know how long in advance. When the stickleback likely disappeared from the lake somewhere between 1957 and early 1960ies due to perch predation, the planktivore pressure therefore declined. Since the brook trout introduction was not successful, their impact on PCC was likely negligible. We therefore conclude that the 1960ies transient dynamics was occurring towards a single species perch population until early 90ies.

The period between 1992 and 2000 is very well studied and shows a strong effect from a perch recruitment cycle (Persson et al. 2004). During this period we can calculate a Planktivore Population Capacity, PPC, which correlates well to the PCC values of this period ( $r^2 = 0.89$ ,  $p < 0.05$ ). During the periods of high PPC, (and PCC) there is a strong yearly recruitment in perch and young-of-the-year perch are very abundant and hence planktivore pressure is high in the lake (Persson et al. 2004). On the other hand, during the years of low PPC (and PCC) the recruitment of young perch is very low and consequently the predation pressure from perch on zooplankton is low.

In this study we conclude that the inferred planktivory, PCC we obtained by using the transfer function based on *Bosmina* remains correlates well to the known history of the fish population in the lake. Still, a more rigorous study and test is needed to verify our conclusions since we here lack data from sediment cores from control lakes where the fish populations have been stable over time.

## Conclusions and future perspectives

The studies in this thesis show that the morphological measurements carapace length and mucro length of *Bosmina* can be used to infer past planktivory in northern Swedish lakes. Furthermore we show that PCC has a higher explanatory power than CPUE in lakes that are dominated by omnivorous fish; we argue this is because PCC takes into account the size- and age-specific planktivory of fish that CPUE ignores. We also show that the morphology of the contemporary *Bosmina* correspond well with the remains found in the sediment dating from the same time period. Both the contemporary and microfossil *Bosmina* changes in body size characteristics was in turn strongly related to our estimates of the intensity of planktivory in the lake, the population planktivore capacity; PPC. Finally, in the resurrection study (paper I) we show that hatching of *Ceriodaphnia* ephippia is promising for studying past planktivory, both because of the high viability of the ephippia and the relationship between eye area and inferred PCC.

The knowledge of how the fish community in a lake has fluctuated over time is of course interesting per se but also of importance for the future management of lakes. Fish leave identifiable remains in the sediment (such as scales, teeth and vertebrae). These remains are, however, scarce (Patterson and Smith 2001, Davidson et al. 2003) and historical



documentation is limited. The paleolimnological methods used here, where we only used one taxon and took two morphological measurements into account, makes the method easy to learn and the analysis fairly quick and simple. We suggest that our method has the potential to quantitatively infer the past history of fish populations in lakes. Hence, this approach should be a valuable complement for e.g. management purposes when reconstructing historical fish communities in lakes is of importance.

The approach of studying long-term population dynamics in fish by inferring PCC corresponded well to known historical changes in the study lake (paper IV). Still a more extensive study is needed to test the hypothesis. In this study we lack data from sediment cores from control lakes where the fish population has been stable over the analyzed time period. These data could likely be used to rule out alternative explanations to our correlative conclusions and suggested patterns of planktivory and changes in the fish community based on historical data.

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# Author contributions

Note: Authors are referred to by their initials

**Paper I:** Reinikainen, M & Åhlén, E. Viability of century old cladoceran ephippia: morphological variation in *Ceriodaphnia quadrangular* under historic changes in predation regimes. *Submitted manuscript*

MR came up with the idea of this paper and developed the study design and methods. MR was also responsible for the manuscript preparation. EÅ was responsible for the palaeolimnological analyses and contributed with the reconstruction of predation pressure (here also used as an indirect dating method). The results and their interpretations were discussed together.

**Paper II:** Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M. Relationships between planktivore community capacity (PCC) and cladoceran microfossils in northern Swedish lakes. - *Fundamental and Applied Limnology* **178**: 315–324

The original idea for this paper was from the application to CMF by MR and PB. The study design was discussed by EÅ, MR and PB. EÅ was responsible for data collection where MR, TK, PB and LP contributed. EÅ did all the palaeolimnological analysis and developed this method. The results and their interpretations were extensively discussed by EÅ, MR, PB, TK and LP. EÅ was responsible for the manuscript preparation with contributions of comments and discussions from MR, PB, TK and LP.

**Paper III:** Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M. Planktivore population dynamics affect body size characteristics of *Bosmina*: evidence from sediment archive and contemporary lake samples. *Manuscript*

Extensive discussions between EÅ, MR, PB, TK and LP resulted in the idea of this paper and the design of the study. The data collection for the palaeolimnological part was done by EÅ, MR, TK and LP and the data for the contemporary zooplankton and fish populations was contributed by LP and PB. The palaeolimnological and zooplankton analysis was done by EÅ. The interpretations of the results were discussed by EÅ, MR, TK, PB and LP. EÅ was responsible for the manuscript preparation with contributions of comments and discussions from MR, PB, TK and LP.

**Paper IV:** Åhlén, E., Byström, P., Korsman, T., Persson, L. and Reinikainen, M. Remains of *Bosmina* in sediments reflects historical changes in fish populations in a northern Swedish lake. *Manuscript*

The original idea for this paper evolved from discussions by EÅ, MR, PB and TK. The data collection was done by EÅ, TK, MR and LP. The palaeolimnological analysis was done by EÅ. The interpretations of the results were done by EÅ, MR, PB and TK. EÅ was responsible for the manuscript preparation with contributions of comments and discussions from MR, PB, TK and LP.

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# Populärvetenskaplig sammanfattning

Fisk har alltid varit en viktig resurs för människan och utgör en betydande del av det biologiska livet i våra sjöar. I de flesta sjöar saknas dock information om hur fiskpopulationer har utvecklats i sjön historiskt. I en del sjöar är det nutida fiskesamhället ofta ett resultat av introduktioner och det är inte känt vad för fisk som fanns i sjön naturligt eller om den rent av var fisktom.

Sjösediment är en form av biologiskt arkiv, allt som produceras i sjön lagras på sjöbotten tillsammans med material som tillförs från atmosfären och avrinningsområdet. Denna sedimentering lagras ovanpå redan befintligt sediment så att sedimentet blir äldre och äldre ju längre ner i sedimentet man gräver. Detta arkiv används för att studera historiska förändringar i sjön så som klimat, sjödjup, pH/försurning, näringshalt/övergödning och försurning. Det man studerar är t.ex. kiselalger, pigment, fjädermygglarver och hinnkräftor. Eftersom fiskar lämnar mycket få rester i sedimentet studerar man istället dess föda, hinnkräftor. Fisk är rovdjur som använder synen och äter i första hand stora och synliga djur. På så sätt förändras djurplanktonsamhället beroende på hur stort graden av planktivori är i sjön.

Denna avhandling utreder möjligheten att använda mikrofossil från hinnkräftan *Bosmina* för att påvisa förändringar i norrländska sjöars fiskesamhällen. *Bosmina* är en lämplig organism att studera eftersom den är ett vanligt djurplankton i våra sjöar, ett viktigt bytesdjur för fiskar och bevaras väl i sjösediment.

En annan målsättning var att hitta ett bättre mått på planktivori än CPUE (antal fisk/nät, fångst per ansträngning) från provfisken. Detta mått är inte tillräckligt bra för sjöar som har fiskesamhällen som ändrar födoval under sitt liv, t.ex. abborre som äter djurplankton som små för att senare växla till insektslarver och till sist bli fiskätare. Det mått som togs fram här, PCC (det planktivora fiskesamhällets kapacitet) tar hänsyn till varje fisks art- och storleks-specifika kapacitet att äta djurplankton.

Denna avhandling visar att PCC är ett bättre mått på planktivori än CPUE i norrländska sjöar som domineras av fisk som inte är specialister på plankton. Den visar också att morfologiska mått på mikrofossil av *Bosmina* från sjösediment är användbar för att rekonstruera forna fiskpopulationers planktivorityck. Vidare stämmer de morfologiska måtten från *Bosmina* provtagna i vattenmassan mycket väl överens med *Bosmina* mikrofossil som sedimenterats i sedimentet under motsvarande tidsperiod. Samma mått från

”hela” *Bosmina* och *Bosmina* skal från sedimentet var väl korrelerat med vårt eget mått på planktivori i en sjö vars fisksamhälle är mycket väl studerat.

Denna avhandling har också undersökt möjligheten att studera planktivori genom att kläcka upp viloägg från *Ceriodaphnia* från sjösediment och mäta dess ögonstorlek. Detta tillvägagångssätt verkar lovande dels för att ögonstorleken var signifikant mindre under perioden med högst rekonstruerat planktivori och dels för att *Ceriodaphnias* viloägg hade en mycket god kläckbarhet ner till 20 år gammalt sediment (ca 5 cm) men enstaka ägg kläcktes ända ner till 115 års sedimentålder (ca 15 cm).

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