Sedimentary zooplankton remains as indicators of lake ecological quality and trophic structure

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CONTENTS

ABSTRACT

To protect and restore lake ecosystems under threats posed by the increasing human population, information on their ecological quality is needed. Lake sediments provide a data rich archive that allows identification of various biological components present prior to anthropogenic alterations as well as a constant record of changes. By providing a longer dimension of time than any ongoing monitoring programme, palaeolimnological methods can help in understanding natural variability and long-term ecological changes in lakes. As zooplankton have a central role in the lake food web, their remains can potentially provide versatile information on past trophic structure. However, various taphonomic processes operating in the lakes still raise questions concerning how subfossil assemblages reflect living communities.

This thesis work aimed at improving the use of sedimentary zooplankton remains in the reconstruction of past zooplankton communities and the trophic structure in lakes. To quantify interspecific differences in the accumulation of remains, the subfossils of nine pelagic zooplankton taxa in annually laminated sediments were compared with monitoring results for live zooplankton in Lake Vesijärvi. This lake has a known history of eutrophication and recovery, which resulted from reduced external loading and effective fishing of plankti-benthivorous fish. The response of zooplankton assemblages to these known changes was resolved using annually laminated sediments. The generality of the responses observed in Lake Vesijärvi were further tested with a set of 31 lakes in Southern Finland, relating subfossils in surface sediments to contemporary water quality and fish density, as well as to lake morphometry.

The results demonstrated differential preservation and retention of cladoceran species in the sediment. *Daphnia, Diaphanosoma* and *Ceriodaphnia* were clearly underrepresented in the sediment samples in comparison to well-preserved *Bosmina* species, *Chydorus*, *Limnosida* and *Leptodora*. For well-preserved species, the annual net accumulation rate was similar to or above the expected values, reflecting effective sediment focusing and accumulation in the deepest part of the lake. The decreased fish density and improved water quality led to subtle changes in zooplankton community composition. The abundance of *Diaphanosoma* and *Limnosida* increased after the reduction in fish density, while *Ceriodaphnia* and rotifers decreased. The most sensitive indicator of fish density was the mean size of *Daphnia* ephippia and *Bosmina (E.) crassicornis* ephippia and carapaces. The concentration of plant-associated species increased, reflecting expanding littoral vegetation along with increasing transparency. Several of the patterns observed in Lake Vesijärvi could also be found within the set of 31 lakes.

According to this thesis work, the most useful cladoceran-based indices for nutrient status and planktivorous fish density in Finnish lakes were the relative abundances of certain pelagic taxa, and the mean size of *Bosmina* spp. carapaces, especially those of *Bosmina (E.) cf. coregoni*. The abundance of plant-associated species reflected the potential area for aquatic plants. Lake morphometry and sediment organic content, however, explained a relatively high proportion of the variance in the species data, and more studies are needed to quantify lake-specific differences in the accumulation and preservation of remains. Commonly occurring multicollinearity between environmental variables obstructs the cladoceran-based reconstruction of single environmental variables. As taphonomic factors and several direct and indirect structuring forces in lake ecosystems simultaneously affect zooplankton, the subfossil assemblages should be studied in a holistic way before making final conclusions about the trophic structure and the change in lake ecological quality.

LIST OF ORIGINAL PAPERS

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

I	Nykänen, M., Kairesalo, T., Mäkelä, S., Huitu, E., Ala-Opas, P. & Mannio, J. 2005: A typology and ecological classification system for Finnish lakes: applicability of the ECOFRAME scheme. *Boreal Environment Research* 10: 159-179.
II	Nykänen, M., Vakkilainen, K., Liukkonen, M. & Kairesalo, T. 2009: Cladoceran remains in lake sediments: a comparison between plankton counts and sediment records. *Journal of Paleolimnology* 42: 551-570.
III	Nykänen, M., Liukkonen, M. & Kairesalo, T. 2006: Changes of predation pressure by fish in Lake Vesijärvi reflected by sedimentary cladoceran remains. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 29: 1321-1326.
IV	Nykänen, M., Vakkilainen, K. & Kairesalo, T. 2008: Rotifer resting eggs in the sediment indicate trophic changes in Lake Vesijärvi. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 30: 441-445.
V	Nykänen, M., Malinen, T., Vakkilainen, K., Liukkonen, M. & Kairesalo, T. 2010: Cladoceran community responses to biomanipulation and re-oligotrophication in Lake Vesijärvi, Finland, as inferred from remains in annually laminated sediment. *Freshwater Biology* 55: 1164-1181.

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THE AUTHOR'S CONTRIBUTION

MK (formerly M. Nykänen) planned each study with contributions from TK and was the corresponding author of all the papers.

I MK was responsible for the field sampling and analysis of 6 lakes and summed the data from the other lakes. SM, EH and PA-O provided data from 17 lakes and JM a data set of 874 lakes. MK performed data analysis, interpreted the results, drew the figures and wrote the paper. The co-authors revised the paper. TK supervised the work.

II MK and ML carried out the field sampling of sediment. ML dated and sliced the sediment cores. KV provided contemporary zooplankton data. MK processed and analyzed the sediment samples, planned and performed the data analysis, interpreted the results, drew the figures and wrote the paper. The co-authors revised the paper. TK supervised the work.

III MK and ML carried out the field sampling of sediment. ML dated and sliced the sediment. MK processed and analyzed the sediment samples and carried out the length measurements. MK planned and performed the data analysis, interpreted the results, drew the figures and wrote the paper. TK supervised the work.

IV MK processed and analyzed the sediment samples. KV provided zooplankton data from water samples. MK planned and performed the data analysis, interpreted the results, drew the figures and wrote the paper. The co-authors revised the paper. TK supervised the work.

V MK and ML carried out the field sampling of the sediment cores. ML dated and sliced the cores. TM provided fish data and KV provided data on water temperature and cyanobacteria. MK processed and analyzed the sediment samples and carried out the length measurements. MK planned and performed the data analysis, interpreted the results, drew the figures and wrote the paper. The co-authors revised the paper. TK supervised the work.

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

ABBREVIATIONS

etc.	et cetera (and so on)
i.e.	id est (that is)
e.g.	exempli gratia (for example)
cf.	confer (compare)
No.	Number
LOI	Weight loss on ignition, used as a surrogate for the content of organic matter in sediment
OM	Content of organic matter in sediment, measured as the weight loss on ignition
DW	Dry weight
TP	Total phosphorus
P	Phosphorus
N	Nitrogen
chl a	Chlorophyll a
BCPUE	Catch per unit effort (CPUE) of fish in multimesh gillnets, expressed as fresh weight of fish (biomass, B)
NCPUE	Catch per unit effort of fish (CPUE) in multimesh gillnets, expressed as numbers (N) of fish
P/L ratio	Ratio of the remains of planktonic species to littoral species
WFD	Water Framework Directive
ANOVA	Analysis of variance
DCA	Detrended correspondence analysis
PCA	Principal component analysis
RDA	Redundancy analysis
VIF	Variance inflation factor

1. INTRODUCTION

1.1 Assessment of ecological quality in lake ecosystems

The increasing human population poses several threats to freshwater ecosystems, ranging from eutrophication, acidification and toxic pollution to erosion and climate change (Wetzel 1992). The Water Framework Directive (WFD; 2000/60/EC) is a legislative framework to protect and restore surface waters in the European Union. It defines 'ecological status' as "*an expression of the quality of the structure and functioning of aquatic ecosystems associated with surface waters.*" The assessment of ecological quality basically requires two elements: a measure of the ecological resource of interest and a reference condition (benchmark) against which to judge whether the measured condition differs from what is expected (Hawkins et al. 2010). Reference conditions are agreed to represent ecological properties associated with natural or pristine conditions, but the definition of pristine is less clear (Bennion et al. 2011). Progressive degradation of lakes over time (e.g. Johansson et al. 2005) may change society's impression of what is natural (Hawkins et al. 2010). Minimally impacted lakes are rare (Bjerring et al. 2008), as even the most remote sites have been subjected to at least atmospheric pollution (Simola et al. 1991; Goto-Azuma & Koerner 2001; Korhola et al. 2002), increased UV radiation (Rautio & Korhola 2002), and global climate change (Douglas et al. 1994). In addition, natural processes such as lake infilling or long-term changes in catchment soils cause gradual, sustained changes in lake ecosystems (Bennion et al. 2011).

The structure and functioning of aquatic ecosystems inherently vary (Carpenter et al. 1987; Søndergaard et al. 2005). Ecological assessment necessitates understanding of how spatial and temporal variations in the distributions and abundances of freshwater biota are related to environmental features (Hawkins et al. 2010). The determination of typologies and type-specific reference conditions is an attempt to control spatial variation resulting from the natural, multidimensional heterogeneity of the environment (WFD; 2000/60/EC). Because variation in landscape features, as well as in biological quality parameters, is gradual rather than stepwise (Jeppesen et al. 2000a,b; Søndergaard et al. 2005; Bennion et al. 2011), *a priori* classifications may fail to effectively partition natural ecological variation. The same concerns temporal variation, which is partly predictable (seasonality), stochastic (extreme events) or system driven. Non-linear responses of organisms operating at different rates as well as complex feedbacks among ecosystem components cause fluctuations, even regime shifts (Carpenter 2003). The site-specific aspect of year-to-year variation, which is an important component of ecological variation, needs to be understood when assessing ecological quality. While fixed-boundary schemes inevitably lead to the wrong classification of some lakes (Moss et al. 2003; Irvine 2004; Søndergaard et al. 2005; Bennion et al. 2011), site-specific approaches should allow the establishment of more accurate criteria for the ecological status of individual sites (Hawkins et al. 2010).

Global climate change (ICCP 2007) further confounds our ability to assess the true ranges of natural variability by affecting the baseline values of reference conditions (Nõges et al. 2007). Climate change may affect biogeochemical processes in catchments or in sediments, as well as the physical environment, including the ice-covered period, mixing patterns and oxygen saturation (e.g. Korhola et al. 2002; Battarbee et al. 2005;

Jankowski et al. 2006; Jeppesen et al. 2009). If the climate-induced timing of key biological events such as spawning, hatching or the growth phases of prey and predator respond differently to increasing temperature, mismatch in the food web may affect the entire ecosystem (Winder & Schindler 2004). All these changes may have a major effect on ecosystem structure and functioning. Jeppesen et al. (2009) predicted that the trophic structure in northern temperate lakes would change towards communities less resistant to external nutrient loading, i.e. a shift in the fish community structure towards small and abundant plankti-benthivorous fish, enhanced predator control of zooplankton and a higher importance of cyanobacteria. Long-term monitoring of minimally impacted sites is therefore important for understanding the effects of climate change on lake ecological status and, in terms of the WFD, possibly changing baseline values (Battarbee et al. 2005: Nõges et al. 2007; Bennion et al. 2011).

Long-term monitoring data are only available for a fraction of lakes, and no lake has been effectively monitored over 200 years, which is a time scale already showing increasing anthropogenic impacts in European lakes (Battarbee et al. 2011; Bennion et al. 2011). Lake sediments provide a data-rich archive that allows the site-specific identification of various biological components present prior to anthropogenic alterations as well as a constant, long-term record of changes (Smol 1992; 2008; Bennion & Battarbee 2007). Subfossil biological assemblages, i.e. remains of past animal and plant communities preserved in sediments (Smol et al. 2001a; 2001b), provide a direct estimate of biotic reference conditions. The prealteration water quality (e.g. pH, total phosphorus concentration, water temperature) for individual lakes can be inferred by using transfer functions (reviewed by Birks 1998) that relate current environmental conditions in a set of lakes to the biotic structure in surface sediments. In the selection of reference sites, sediments can be used to prove that the ecological quality parameters in a selected lake have remained more or less unchanged during the period of anthropogenic influence (cf. Räsänen et al. 2006; Bjerring et al. 2008). By providing long-term data, essential for detecting climatic and other effects, palaeolimnological methods can help to answer questions about natural variability, and to redefine the baseline conditions (Anderson 1993; Battarbee et al. 2005). As palaeolimnological methods develop, they are increasingly being used together with neolimnological data to understand long-term ecological changes in lakes, and even to test ecological theories (Smol 1990; Sayer et al. 2010). Interpretation of the sediment record is not straightforward, however, and efforts to improve the comparability of observational data and the palaeolimnological record are still needed (Battarbee et al. 2005).

1.2 Role of zooplankton in the structure and functioning of lake ecosystems

Zooplankton, by grazing on phytoplankton and other seston, recycling nutrients and organic material, and serving as prey for vertebrate and invertebrate planktivores, are a key element regarding the structure and functioning of lake ecosystems (cf. Jeppesen et al. 2011). Algae–zooplankton interactions form the basis for energy flux to higher trophic levels. In the majority of lakes, the availability of phosphorus limits algal production and hence also the level of secondary production (Hessen et al. 2006). With enhanced nutrients, the total zooplankton biomass increases, especially the abundance of rotifers, cladocerans and cyclopoid copepods (Vanni 1987). The ratio between zooplankton and phytoplankton biomass decreases, however, indicative of poorer grazer control of phytoplankton (McCauley & Kalff 1981; Pace 1986; Jeppesen et al. 2000a; 2003a; Søndergaard et al. 2005). Although phytoplankton become more abundant, their quality as food for zooplankton may deteriorate because the proportion of large, inedible forms of algae increases (Watson & Kalff 1981; Watson et al. 1997).

In the absence of fish, large zooplankton species, especially *Daphnia,* have a competitive advantage over small species. Large *Daphnia* are more efficient competitors for resources than small species. They have a higher per-capita filtering rate, a broad diet, lower metabolic demands per unit mass, better resistance to starvation, and they have a high reproductive rate owing to high fecundity attained by large clutch sizes (Goulden et al. 1978; Peters & Downing 1984; Gliwicz 1990a). As the availability of nutrients increases, large colonial and filamentous algae, and even toxic forms of cyanobacteria increase in abundance (Watson et al. 1997). They are more resistant to grazing and may interfere in the feeding of large species more than that of small species, which feed selectively on a narrower size range of food particles (Webster & Peters 1978; Lampert 1982; Hawkins & Lampert 1989). Therefore, large species may lose their competitive advantage over small, less efficient grazers at high nutrient concentrations (Rothhaupt 1990).

The competitive advantage of large, efficient grazers in lakes is often lost because of planktivorous fish. With enhanced primary production, the abundance of planktivorous and benthivorous cyprinid fish increases, while the relative proportion of piscivores decreases, and the size distribution shifts towards small fish (Jeppesen et al. 2000a,b; Olin et al. 2002; Søndergaard et al. 2005). Visually hunting planktivore fish, both obligate and facultative, selectively feed on large, more conspicuous prey items (Zaret 1975; Hall et al. 1976; O'Brien 1979). This size selection is related to the optimal allocation of time and energy spent searching for and handling the prey (Pyke et al. 1977), and is therefore less pronounced if prey densities are low. In addition to the size and density of the prey, a transparent body, a conspicuous eye and the movements of the prey, as well as the turbidity of water affect the prey selection of fish (Zaret 1975; Zaret & Kerfoot 1975; O'Brien 1979; Kitchell & Kithcell 1980). It has been hypothesised that although the population growth rate is mainly determined by resources (bottom-up), each species has its own population density threshold, which is determined by the size at first reproduction and the reactive distance of visually hunting fish (Gliwicz 2001; 2002). This phenomenon could explain relatively stable, 'species-specific' population density levels observed in many lakes (Gliwicz et al. 2000). Under heavy fish predation, small species prevail, because they are able to reproduce at a small size, still being relatively unsusceptible to predation (Lynch 1980).

In contrast to fish, invertebrate predatators, such as C*haoborus*, copepods, *Leptodora* and *Bythotrephes,* select smaller prey, and predation is mostly tactile (Kerfoot 1978; 1981; O'Brien & Schmidt 1979; Branstrator 1998; Sakamoto et al. 2007). Therefore, selection forces posed by fish and invertebrate predators differ, as rapid growth and a large size are advantageous in invertebrate predation (Zaret 1975; Lynch 1980). The major importance of predation on cladocerans can be seen in a variety of evolutionary adaptations against predators. Cyclomorphosis (Lagergren & Stenson 2000), the elaboration of spines or other body shapes, increases the handling time for predators (Kerfoot 1978; Sakamoto et al.

2007; Sakamoto & Hanazato 2008); diurnal migrations take advantage of hypolimnetic or littoral refugia (Zaret 1975; Zaret & Suffern 1976; Lampert 1989; Jeppesen et al. 1998), and "dead man response" provides one last escape mechanism (Kerfoot 1978). Life history traits, such as the size at first reproduction, are important aspects of evolution in cladocerans (Lynch 1980) and, in addition to a genetically determined component, involve marked phenotypic plasticity, which is responsive to a changing predation regime (Vanni 1987; Macháček 1991; Stibor 1992).

The importance of fish in the regulation of size structure and species composition of zooplankton is well documented (Hrbáček et al. 1961; and several studies thereafter) and, together with aspects of interspecific competition, has been formulated as a size-efficiency hypothesis (Brooks & Dodson 1965; Hall et al. 1976). The trophic cascade theory, in turn, assumes that the effects of consumers at the top of the food chain cascade down to the producer level (Carpenter et al. 1985). Although nutrients determine the level of phytoplankton growth, much of the variation in phytoplankton is explained by food-web interactions (Mazumder 1994). The significant implications of trophic cascades for food-web structure have led to attempts to suppress nuisance algae by manipulating the higher trophic levels (termed biomanipulation; Shapiro et al. 1975; Shapiro & Wright 1984). The removal of planktivorous fish, either directly or by stocking piscivores, allows the populations of large herbivorous zooplankton to increase and promote a higher grazing pressure on phytoplankton, ultimately resulting in lower algal turbidity. Nutrient regeneration of planktonic animals is important, especially in pelagic food webs (Helminen & Sarvala 1997; Hudson et al. 1999). Fish-mediated changes in the zooplankton community structure could also affect the rate and the elemental ratio at which nutrients are recycled. Small species with higher mass specific metabolic rates recycle nutrients at a higher rate than large species (Bartell & Kitchell 1978; Bartell 1981). *Daphnia* has high physiological requirements for phosphorus, and a *Daphnia*-dominated community could therefore lead to a higher N:P ratio of recycled nutrients than a community dominated, for instance, by calanoid copepods (Andersen & Hessen 1991; Elser et al. 1996). This could have implications for phytoplankton composition, as a low N:P ratio favours cyanobacteria (Smith 1983). The evidence for zooplankton-driven stoichiometry affecting the phytoplankton biomass is scarce, however, and difficult to separate from grazing effects (Sterner et al. 1992; Cyr & Curtis 1999).

Biomanipulation has been widely applied in temperate lakes, both with successes and failures. The results have often been short-lived, and sometimes the improvements in water quality have been unrelated to zooplankton grazing (DeMelo et al. 1992; McQueen et al. 1992; Hansson et al. 1998; Drenner & Hambright 1999; Sarvala et al. 2000; Benndorf et al. 2002; Gliwicz 2005; Søndergaard et al. 2007). Although relatively strong 'top down' effects have been seen in experimental treatments, these forces appear weaker on the basis of the food web, indicating strong control by resources, i.e. 'bottom-up' effects (McQueen et al. 1986). Sustained potential productivity and compensatory mechanisms in the food web after fish removal (e.g. recruitment of young fish, possible expansion of invertebrate predators) (McQueen et al. 1992; Ramcharan et al. 1995; Persson 1999; Gliwicz 2005) imply that long-lasting results require sustained fishing efforts and a sufficient reduction of the external nutrient loading, the primary cause of eutrophication (Hansson et al. 1998; Kairesalo et al. 1999; Wetzel 2001;

Søndergaard et al. 2007). Biomanipulation as a management tool is no longer considered solely as manipulation of the pelagic food-chain, but it also integrates benthic pathways in the whole lake processes. Fish reduction directly lowers fish-mediated phosphorus inputs through benthic–pelagic coupling, and expansion of macrophyte cover with increased water clarity can reinforce the clear water state through various feedback mechanisms (Horppila et al. 1998; Schindler & Scheuerell 2002; Vadeboncoeur et al. 2002). Macrophytes exert a major structuring force in shallow lake ecosystems, controlling excess algal growth and providing habitats for a variety of species, including several cladocerans, either strictly substrate-associated, or mainly planktonic, which benefit from macrophyte beds as refugia (Timms & Moss 1984; Scheffer et al. 1993; Jeppesen et al. 1998).

Eutrophication, especially the non-point source loading of phosphorus, is still a major threat to the ecological quality of lakes in Finland and elsewhere (Räike et al. 2003; Schindler 2006). Owing to efficient conservation measures, however, several lakes in Europe and North America are now in the phase of re-oligotrophication. The effects of re-oligotrophication on zooplankton communities are yet to be adequately addressed, and the processes behind re-oligotrophication are still poorly understood (Battarbee et al. 2005). Although understanding and the management of eutrophication have greatly advanced in recent decades, the ecological response of an individual lake to management seems to depend on the complexities of the communities (Schindler 2006). Long-term data are essential to understand the ecological changes in lakes, as multiple stressors and processes operating at different time scales together with dynamic feedback mechanisms may not always lead to the most obvious end result in the course of lake management and re-oligotrophication (cf. DeAngelis et al. 1989; Anderson & Battarbee 1994; Manca & Ruggiu 1998; Jeppesen et al. 2005; Perga et al. 2010).

1.3 Sedimentary zooplankton remains

Deposition of zooplankton remains

Cladocerans are best preserved of zooplankton in lake sediments (Deevey 1964; Frey 1986; Hofmann 1987; Korhola & Rautio 2001). As arthropods, cladocerans grow by periodically shedding their exoskeletons at the end of each instar. Moulting rates differ among species and are largely influenced by temperature (Vijverberg 1980). In addition to the corpses of dead animals, shed exuviae make up a large proportion of the remains that accumulate in the bottom mud (Deevey 1964; Kerfoot 1981). Cladoceran reproduction is mainly parthenogenetic, but ephippia, sexually produced resting stages, are also identifiable. Rotifers are only occasionally preserved, but the resting eggs of rotifers can be found in sediments (Merkt & Müller 1999; van Geel 2001). Copepods are generally poorly preserved (Frey 1986; Rautio et al. 2000), although the shells of eggs have sometimes been reported (Knapp et al. 2001). Protozoans may not be preserved, but some species are relatively well preserved, chiefly testate amoebae (Beyens & Meisterfeld 2001).

After death or the discarding of exuviae, mechanical, chemical and biological processes in lakes fragment, digest or decompose zooplankton remains before their final burial in sediments (Kerfoot 1995; Fig. 1). Although cladocerans are generally well preserved, preservation differs between species (Deevey 1964; Frey 1986; Hofmann

1987; Rautio et al. 2000; Korhola & Rautio 2001; Kattel et al. 2007; Kattel 2009). While Bosminidae and Chydoridae are represented as head shields, carapaces and postabdomens, only postabdominal claws, mandibles, segments of exopodites or fractions of carapace are found for Daphniidae, Sididae, Holopedidae and Macrothricidae. Leptodoridae, Polyphemidae and Cercopagidae are represented as mandibles and caudal projections. The differences are attributable to the thickness and chemical structure of chitin, which vary between the body parts (Deevey 1964). There are also differences in the preservation of cladoceran remains among lakes, but these differences have not been adequately quantified (but see e.g. Flower 1993 for diatoms). The oxygen content of the sediment influences microbial mineralization rates, as well as the distribution of sediment-feeding benthic invertebrates, which both suggest better preservation in anoxic sediments (Anderson & Battarbee 1994). The differential preservation of species has been widely recognized and also studied, but few investigators have tried to quantify the relationship between the actual production of remains and their deposition (Kerfoot 1981, 1995; Hall & Yan 1997).

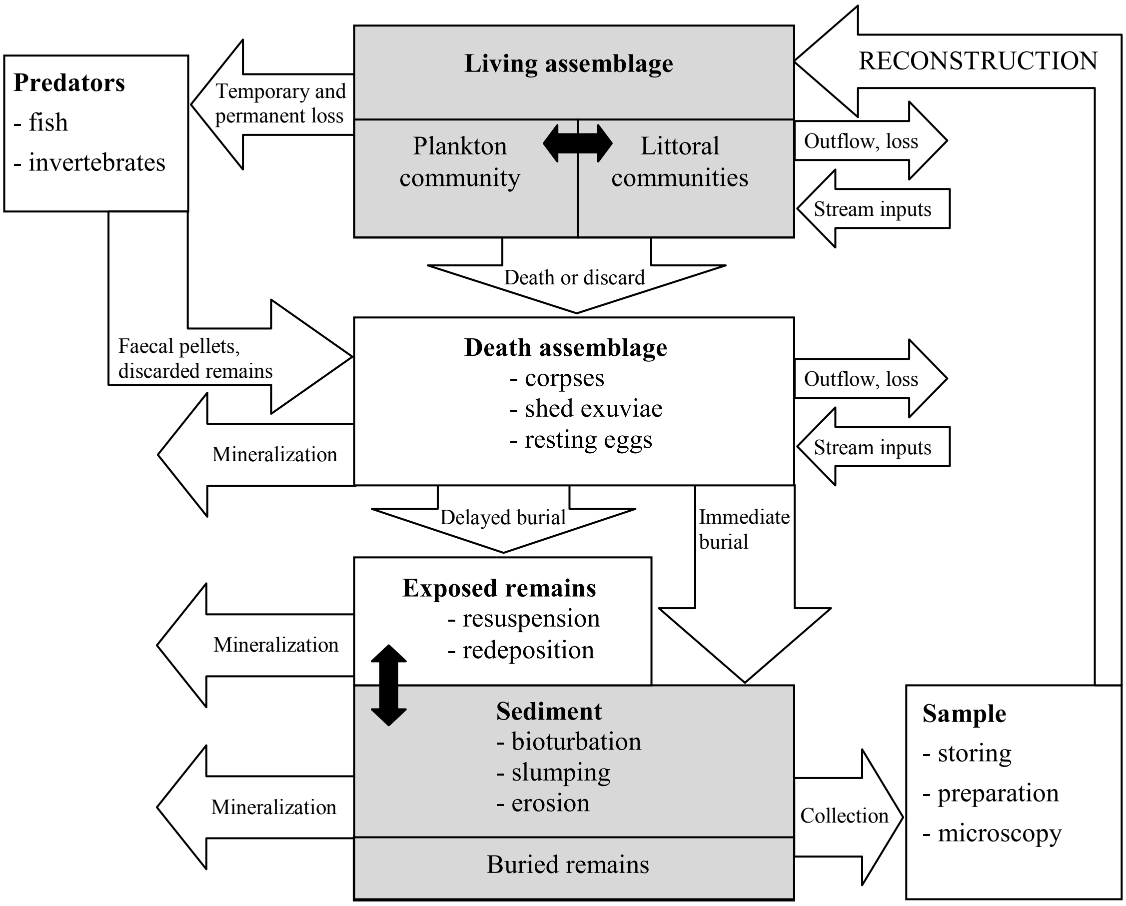

Figure 1. Taphonomical factors affecting zooplankton remains in lakes. Modified from figures of Anderson & Battarbee (1994), Behrensmeyer & Kidwell (1985) and Behrensmeyer et al. (2000).

Sediment samples for cladoceran analysis are usually taken in the central or deepest area of a lake, which forms the most undisturbed zone of accumulation (Håkanson & Jansson 1983). Because of a process known as sediment focusing, this area has been thought to integrate temporally and spatially separate populations of cladocerans in the lake, even to the extent that more species can be found in a sediment sample than in an extensive, several year sampling of live populations (Frey 1960). However, Kattel et al. (2007) demonstrated that a central sediment core represents well the pelagic populations, whereas the integration of remains from littoral source communities is highly variable. The eventual species composition in deepwater sediment depends on the spatial distribution of littoral and pelagial cladoceran populations together with transport–sedimentation processes in the lake (Hofmann 1987; 1998; Whiteside & Swindoll 1988; Rautio et al. 2000; Kattel et al. 2007), which are greatly dependent on lake morphometry (Lehman 1975; Hilton et al. 1986; Blais & Kalff 1995). Understanding of the sedimentation pattern at a coring site is crucial for the interpretation of the sediment record (Räsänen et al. 1992; Anderson & Battarbee 1994). Lake-specific factors certainly cause variation among lakes, but these same factors may also affect the signal in an individual lake, if water level, and hence the sedimentation patterns, or the relative importance of littoral and pelagic habitats, change. In fact, the ratio of planktonic to littoral species (P/L ratio) has been used to indicate water level changes (Alhonen 1970; but see Hofmann 1998). The relative importance of these habitats may also vary without changes in the water level, especially in shallow lakes, where the changes in transparency affect benthic production in large bottom areas (Scheffer et al. 1993).

As several factors affect the deposition of cladoceran remains, the resulting subfossil community in deep water sediment, the main interest of a palaeolimnologists, may be a quite biased reflection of living communities, confounding the direct interpretation of species abundances (Rautio et al. 2000; Kattel et al. 2007). Therefore, the reliability of the sediment record still concerns palaeolimnologists. Taphonomy is the study of the ways in which preservation affects the fossil record. Taphonomic processes begin at death or discard, and continue with preburial, possible exposure and concentration, to final burial in the sediment (Fig. 1). Sample collection, preparation and analysis may introduce further biases, and are thus an integral part of taphonomy (Behrensmeyer & Kidwell 1985; Behrensmeyer et al. 2000).

Several researchers have assessed the compositional or temporal fidelity of sedimentary remains, but the methods used are not directly comparable. The methods include the comparison of samples of live animals with surface sediment or trap samples (Kerfoot 1981, 1995; Hall & Yan 1997; Rautio et al. 2000; Kattel et al. 2007), the comparison of sediment trap material with core-top samples (Kattel 2009), multilake comparisons of zooplankton and surface sediment samples (Verschuren & Marnell 1997; Jeppesen et al. 2003b; Davidson et al. 2007) and comparisons of well-dated or annually-laminated sediments with historical zooplankton records (Pražáková & Fott 1994; Leavitt et al. 1989; 1994; Hann et al. 1994; Jankowski & Straile 2003; Manca et al. 2007; Hauptfleisch et al. 2010). The latter are of particular importance, as they allow testing of the reliability of palaeolimnological studies aiming at the reconstruction of temporal patterns in lakes. Lakes having both annually laminated sediment and long-term zooplankton monitoring data are, however, relatively rare.

Sedimentary zooplankton remains as indicators of trophic structure

Despite taphonomical concerns, the analysis of cladoceran remains in lake sediments has proven invaluable for evaluating the response of a lake to various environmental stressors, such as eutrophication, acidification or climate change (Szeroczyńska 1998; Korhola & Rautio 2001; Jeppesen et al. 2001b; Amsinck et al. 2007). Chydoridae, a species-rich family of mostly littoral cladocerans, is widely used in palaeolimnological studies. Chydorids leave well-preserved, identifiable remains (Frey 1959), and the species occurrences have been related to various chemical conditions or littoral habitat types (e.g. Whiteside 1970; Hann 1989; Flössner 2000; de Eyto et al. 2003). Most cladoceran species are found in a wide variety of lake types, and community compostion as a whole is therefore a more reliable predictor of lake conditions than the occurrence of a single species (Korhola & Rautio 2001). The remains of pelagic species, chiefly *Daphnia* and *Bosmina,* have especially been used when interpreting historical changes in trophic structure (e.g. Kitchell & Kitchell 1980; Kerfoot 1981; Leavitt et al. 1989; 1994; Brodersen et al. 1998; Jeppesen et al. 2001a; Manca et al. 2007). Although some scales of fish may preserve in sediments (Davidson et al. 2003), they are generally scarce and the reconstruction of past fish communities would demand an appreciably large amount of sediments. The widely recognised effects of fish predation on zooplankton provide an indirect means to assess changes in past fish communities.

Several indices or ratios, based on pelagic cladocerans, have been used as indicators of lake trophic status and planktivorous fish density. These include the ratio *Daphnia*/(*Daphnia*+*Bosmina*) (e.g. Kitchell & Kitchell 1980; Leavitt et al. 1989; 1994; Hann et al. 1994; Jeppesen et al. 2003b; 2011), and to a lesser extent, the ratio rotifer resting eggs/(rotifers+planktonic cladocerans) (cf. Guilizzoni et al. 2006). Size measurements of *Daphnia* and *Bosmina* remains (Kitchell & Kitchell, 1980; Salo et al. 1989; Hann et al. 1994; Verschuren & Marnell 1997; Jeppesen et al. 2002; Sweetman & Finney 2003; Perga et al. 2010) have been used to track fish predation effects, while the length and shape of *Bosmina* mucros and antennules have been related to invertebrate predation (Kerfoot 1981; Sanford 1993; Hann et al. 1994; Manca et al. 2007). Size measurements have even been used as a regional indicator of ecosystem change and zooplankton community composition (Korosi et al. 2010; Alexander & Hotchkiss 2010).

Trophic changes may also have implications for the ephippium production of cladocerans (Jankowski & Straile 2003). The ephippium percentage [ephippia/(parthenogenetic remains + ephippia) × 100%] has been used to infer temperature changes or environmental stress (Sarmaja-Korjonen 2003; 2004). As ephippia are a regular strategy for overwintering in several cladoceran species, longer growing seasons could lead to prolonged periods of parthenogenetic reproduction and, consequently, to a lower ephippium% (cf. Jeppesen et al. 2003b; Sarmaja-Korjonen 2003; 2004; Tsugeki et al. 2008). As diapausing eggs can remain viable for decades, even centuries, dated egg banks can reveal evolutionary changes in cladoceran populations (Weider et al. 1997; Hairston et al. 1999).

The use of cladoceran remains in reconstructing environmental conditions and trophic structure has proceeded from descriptive studies to quantitative reconstructions in concert with the general development of palaeo-limnological methods, especially of coring techniques, dating and statistical methods (Birks 1998; Smol 2008).

Quantitative predictive models (transfer functions) based on cladoceran remains have already been developed to reconstruct past fish density (Jeppesen et al. 1996; Amsinck et al. 2005), submerged macrophyte coverage (Johansson et al. 2005; Bjerring et al. 2008), total phosphorus (TP) (Lotter et al. 1998; Brodersen et al. 1998), pH (Krause-Dellin & Steinberg 1986; Huttunen et al. 1988), water colour (Huttunen et al. 1988), salinity (Bos et al. 1999), lake depth (Bos et al. 1999; Korhola et al. 2000; Amsinck et al. 2006) and mean summer air or surface-water temperature (Lotter et al. 1997; Korhola 1999; Kattel et al. 2008). Although transfer functions are a powerful means to predict environmental conditions, and perform well in certain situations, problems may arise. Cladocerans are simultaneously affected by several direct and indirect factors in lake ecosystems, and the error of prediction for a single variable in transfer functions can therefore be high (Davidson et al. 2010b). The application of such models may even lead to false predictions of lake ecological quality, if used alone without a wider consideration of ecosystem-level changes, as shown by Sayer et al. (2010) with a diatom-based transfer function for TP. Recent studies have applied semi-quantitative methods and regression trees, which accommodates the problem of multiple structuring forces, and allows the reconstruction of several factors simultaneously (Amsinck et al. 2006; Bjerring et al. 2009; Davidson et al. 2010a,b). There is an urge to get 'back to basics', and consider more fully the niche dimensions and ecology of subfossil species (Birks & Birks 2006), and not to ignore qualitative approaches informed by contemporary data on species' habitat preferences, seasonality, feeding strategies and interactions (Sayer et al. 2010).

2. OBJECTIVES OF THE PRESENT STUDY

This thesis work aimed at improving the use of sedimentary zooplankton remains as indicators of lake ecological quality and trophic structure. Eutrophication, i.e. antropogenic enrichment of waters by nutrients, is still a major threat to the ecological status of lakes in Finland and elsewhere in the world (Räike et al. 2003; Schindler 2006). The focus of this thesis is on nutrient status and planktivorous fish density, and the related changes in zooplankton community in lake pelagial.

The thesis begins with an introduction to ecological quality classification. The first paper (I) concentrates on a pan-European typology and classification system developed in the EU project ECOFRAME (Moss et al. 2003). By testing the applicability of the system with a Finnish lake set, the paper highlights the characteristics of Finnish lakes, as well as the practical problems involved in assessing ecological quality using fixed-boundary schemes.

Palaeolimnogy provides long-term data on the ecological changes in lakes and, in the context of ecological quality assessment, has been offered as a tool to determine the undisturbed background conditions as well as site-specific solutions for ecological quality assessment (Bennion et al. 2007; 2011; Hawkins 2010). The correct interpretation of palaeolimnological records demands both understanding of the ecological significance of observed changes, and understanding of the taphonomical processes that affect the signal. So far, these processes have not been fully understood for cladoceran remains (Kattel 2009). Few investigators have quantified the relationship between the production of remains and their deposition, taking into account species-specific moulting rates (Kerfoot 1981, 1995; Hall & Yan 1997), and even fewer have done this simultaneously for several species to quantify interspecific differences. The second paper of this thesis (II) focuses on the taphonomy of cladoceran remains, and quantifies interspecific differences in the retention and accumulation of remains of nine pelagic taxa in the sediment of Lake Vesijärvi, located near Lahti in southern Finland. The thick annual laminations of the sediment together with several years of zooplankton monitoring data enabled a year-to-year and even a seasonal comparison of living communties and their subfossil remains.

Papers III, IV and V examine, by using annually laminated sediment, the response of the subfossil zooplankton community to known changes in fish density and water quality in Lake Vesijärvi. This culturally eutrophicated lake suffered from cyanobacterial blooms that persisted despite reductions in the external nutrient input. Biomanipulation, a major reduction of plankti- and benthivorous fish, led to improved water quality and the disappearance of cyanobacteria. Because zooplankton monitoring data are insufficient from that period, the aim of this thesis work, by using sedimentary zooplankton remains, was to obtain a continuous data set and understanding of long-term changes in the zooplankton community during the biomanipulation and the subsequent recovery-phase. At the same time, the major fish reduction provided an opportunity to directly observe how the sedimentary cladoceran remains and various cladoceran-based indices (cf. Jeppesen et al. 2001b; 2011) reflect changes in lake nutrient status and fish density.

To test the generality of the conclusions based on data gathered from Lake Vesijärvi, additional, unpublished material is presented in this thesis. Surface sediments were sampled and subfossil cladocerans were analysed from 31 lakes in southern Finland with known water quality and fish density. The aim was to attain a broader understanding of factors structuring pelagic cladoceran assemblages in lakes in southern Finland, and to assess the importance of fish density in relation to other factors.

The main questions addressed by this thesis research were:

1. Are there species-specific differences in the preservation, retention or accumulation of pelagic cladoceran remains in lake sediment? (II, synopsis)
2. How does the pelagic zooplankton community change along a trophic gradient, inferred from lake sediments? (IV, V, synopsis)
3. Which cladoceran-based indices or ratios can be used as a proxy for change in lake trophic structure? (I; V, synopsis)
4. To what extent does the mean size of *Daphnia* ephippia and *Bosmina* ephippia and carapaces reflect changes in fish predation? (III, V, synopsis).

3. MATERIAL AND METHODS

3.1 Study sites

Lake Vesijärvi – a lake with fish manipulation and annually laminated sediment

Lake Vesijärvi in southern Finland is a relatively large (110 km^2) and shallow (mean depth 6 m) lake, which has originally been an oligohumic, clear-water lake with naturally eutrophic characters due to a fertile catchment (Keto & Sammalkorpi 1988). The main study area of this thesis (II–V; Figs 2 and 3), Enonselkä basin (26 km^2, mean depth 6.8 m, max depth 33 m), is the most eutrophic of the four basins of Lake Vesijärvi. The basin became culturally eutrophicated along with the growth of the city of Lahti. In the 1960s and 1970s the basin was heavily eutrophicated and experienced persistent cyanobacterial blooms. Coregonids declined and roach (*Rutilus rutilus* (L.)) and other commercially less valuable fish species became dominant (Keto & Sammalkorpi 1988).

Municipal sewage load was diverted from the lake in 1976 and industrial waste in the 1980s, but cyanobacterial blooms persisted (Keto & Sammalkorpi 1988). Roach played a key role in maintaining high productivity (Horppila & Kairesalo 1992). Populations of roach and European smelt (*Osmerus eperlanus* (L.)) were reduced by efficient trawling in 1989−1993, when a total of 1000 tonnes of fish (392 kg ha^{-1}) were caught in the Enonselkä basin (Horppila & Peltonen 1994; Peltonen et al. 1999a, 1999b; Kairesalo et al. 1999). Along with fish removal, the cyanobacterial populations collapsed, epilimnetic total phosphorus decreased, the ratio of chlorophyll-a to total phosphorus decreased, water transparency increased and submerged macrophytes expanded to greater depths (Venetvaara & Lammi 1995; Horppila et al. 1998; Kairesalo et al. 1999; Keto & Tallberg 2000; Vakkilainen 2005). Continued management fishing and stocking of pikeperch (*Sander lucioperca* (L.)) prevented a new increase in planktivorous fish (Kairesalo et al. 1999; Ruuhijärvi et al. 2005).

Improved water quality persisted until the late 1990s, when new signs of deterioration appeared, such as higher turbidity (Kairesalo & Vakkilainen 2004; Keto et al. 2005). The annual roach catch targeted by managers (50 tonnes year^{-1}; Horppila & Peltonen 1994) was not achieved after 1997, but in 2000 management fishing was intensified and the roach population remained low (Ruuhijärvi et al. 2005). The reasons for the degraded status are not completely known but probably involve multiple stressors, such as hot summers and heavy rains, increased external diffuse loading and atmospheric fallout, as well as lakeshore building, which intensified after the recovery of the lake in the 1990s (Kairesalo & Vakkilainen 2004; Keto et al. 2005).

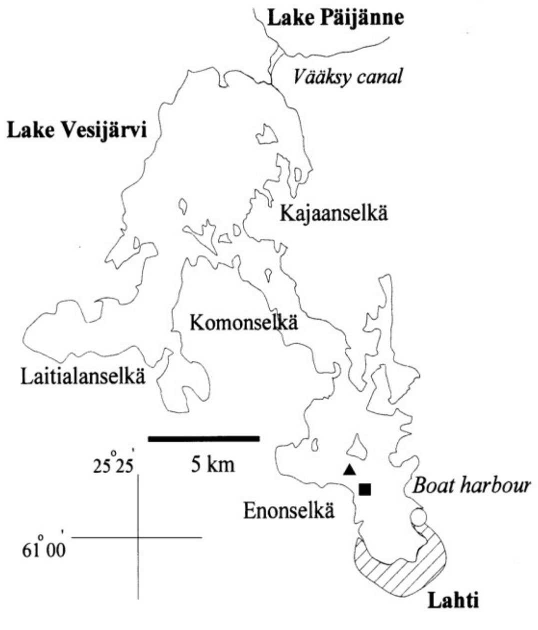

Figure 2. A map of Lake Vesijärvi showing the sediment (triangle; II–V) and zooplankton (square; II) sampling sites.

The deepest part of the Enonselkä basin of Lake Vesijärvi has a high sedimentation rate (average net accumulation in 1985–2002 was 2 cm a^{-1}), and the sediment is annually-laminated. Varve formation is a result of anoxic conditions in the hypolimnion during winter and summer stratification (Liukkonen et al. 1993), which remained a common phenomenon even when the status of the lake improved (Kairesalo & Vakkilainen 2004; Keto et al. 2005). Thick annual laminations provided an exellent opportunity to track changes in the Lake Vesijärvi foodweb using sedimentary zooplankton remains.

Three test sets of lakes: typology, classification and surface sediment

To explore the characteristics of Finnish lakes with a view to their typology (I), a dataset of the joint Nordic Lake Survey was used, including 874 lakes in Finland (Henriksen et al. 1996; 1997; 1998, Mannio et al. 2000). Information required to test the typology developed in the pan-European project ECOFRAME (Moss et al. 2003) was available for 821 lakes. The lakes were randomly selected from national lake registers with a requirement that at least 1% of the lakes (>4 ha) in each region in Finland and all large lakes (>100 km^2) were included. Further details of the lake set can be found in Henriksen et al. (1996; 1997; 1998) and Mannio et al. (2000). A figure illustrating the areal distribution of the lakes can be found in paper I.

A set of 25 lakes (Fig. 3), for which chemical and biological data were available, was collected to test the pan-European ecological quality classification scheme developed by Moss et al. (2003; I). Six of the lakes were studied during the ECOFRAME-project (further details in Moss et al. 2003; Gyllström et al. 2005; Nõges et al. 2003). A total of 17 lakes were studied in a regional project in

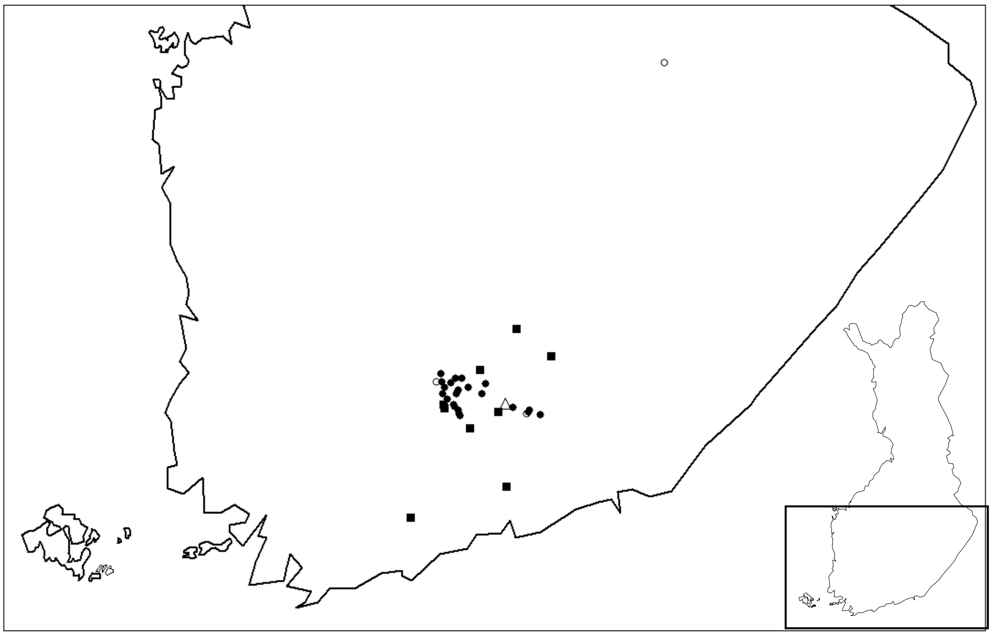

Figure 3. A map of Finland showing the areal distribution of study sites: Lake Vesijärvi (triangle; II–V), 25 lakes used in ecological classification (circles; I), and 31 lakes analysed for surface sediments (filled symbols; synopsis).

Lammi and Tuulos municipalities (Eeva Huitu, Suvi Mäkelä, Pasi Ala-Opas) and information for the remaining lakes was collected from various research reports (for detailed references see paper I). The lakes varied from small oligotrophic forest lakes to eutrophic lakes in agricultural or urban areas. More details of the general characteristics of this lake set can be found in paper I.

To test the generality of the conclusions based on the results from Lake Vesijärvi sediment, surface sediments were collected from 56 lakes in southern Finland, 31 of which were selected for cladoceran analysis. The majority of the selected lakes (22) were the same as in the data set used to test the lake classification (Fig. 3). Two more lakes were selected from the regional project in the Lammi and Tuulos area; five lakes were studied in a regional, EU-funded project on the management and restoration of lakes in Päijät-Häme, and remaining two lakes were investigated in a HOKA project (*Effects of biomanipulation in Finnish lakes*, involving Finnish Game and Fisheries Research Institute, Finnish Environment Institute, University of Helsinki and local authorities). All selected lakes were situated in southern Finland (Fig. 3) to minimize the influence of climate and possible areal differences in the distribution of species. However, the lakes differed in size, depth, water colour and nutrient level, as well as in fish density (Tables 1 and 2).

Table 1. Summary statistics of the environmental variables measured from the 31 study lakes in southern Finland. The last column lists the transformations used in statistical analysis.

Parameter	Mean	Median	Minimum	Maximum	Transformation
LOI % (loss on ignition)	35.6	34.1	11.1	82.4	square root
Surface area, ha	99	43	8	653	log(x)
Mean depth, m	3.3	3.2	1.2	10.7	log(x)
Maximum depth, m	7.8	7.0	2.0	28.0	log(x)
Secchi depth/mean depth	0.6	0.6	0.2	1.4	-
pH	6.8	6.8	6.0	8.4	-
Alkalinity, mmol/l	0.293	0.232	0.052	0.676	square root
Conductivity, µS/cm	78	63	22	158	log(x)
Colour, mg/l	10.1	8.3	1.4	40.1	log(x)
Total nitrogen, µg/l	771	698	265	1868	log(x)
Total phosphorus, µg/l	27.2	22.6	5.5	83.1	log(x)
Secchi depth, m	1.8	1.5	0.6	5.3	log(x+1)
Fish size, g/ind.	23.2	22.2	8.8	67.5	log(x)
Planktivorous fish B, g/net	836	612	33	3581	log(x)
Benthivorous fish B, g/net	387	288	17	1331	log(x)
Piscivorous fish B, g/net	309	212	64	879	log(x)

Table 2. Pearson correlation matrix ($p < 0.05$; ns = not significant) for the transformed environmental variables.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
1. LOI %															
2. Surface area	-0.56														
3. Mean depth	ns	ns													
4. Maximum depth	ns	ns	0.93												
5. Secchi/mean depth	0.36	ns	-0.44	ns											
6. pH	-0.48	0.53	ns	ns	ns										
7. Alkalinity	-0.65	0.54	ns	-0.39	ns	0.80									
8. Conductivity	-0.76	0.52	ns	ns	ns	0.70	0.94								
9. Colour	ns	ns	ns	ns	-0.42	ns	ns	ns							
10. Total nitrogen	-0.52	ns	-0.37	-0.40	-0.43	ns	0.61	0.62	0.41						
11. Total phosphorus	-0.45	ns	ns	ns	-0.56	0.54	0.58	0.52	ns	0.76					
12. Secchi depth	0.51	ns	0.44	0.49	0.58	ns	-0.52	-0.53	-0.59	-0.79	-0.77				
13. Fish size	0.54	ns	ns	ns	ns	ns	-0.49	-0.57	ns	ns	ns	ns			
14. Planktivorous fish B	ns	ns	-0.51	-0.52	ns	0.60	0.61	0.48	ns	0.51	0.61	-0.49	ns		
15. Benthivorous fish B	ns	ns	ns	ns	ns	ns	ns	ns	-0.50	ns	ns	ns	ns	ns	
16. Piscivorous fish B	ns	ns	-0.41	ns	ns	ns	ns	ns	ns	ns	0.37	ns	ns	0.48	0.45

3.2 Sediment analysis

Sediment cores were taken with a freeze-crust sampler at the deepest point (33 m) of the Enonselkä basin of Lake Vesijärvi in January 2003 (II–V). Mikko Liukkonen determined the exact positions of the varves on the basis of the seasonal occurrence of specific diatom species on tape-peel slides (cf. Simola 1977; Liukkonen et al. 1993; 1997; 2006). The beginning of the spring diatom maximum served as a cut-off for the annual varves. The varve thickness was recorded to allow the calculation of annual net sediment accumulation. More details on the dating and slicing can be found in paper II. Material was used from three cores taken from the same general area: The uppermost layers (0−20 cm, 1991−2002) were analysed from core A, which was dated and sliced so that each sample represented one year (II–V). The layers below 20 cm (older than 1991; III–V) were analysed from a longer core C, which was similarly dated and sliced. A known time horizon, a clearly visible clay layer caused by dredging of the boat harbour on the eastern shore of the Enonselkä basin in autumn 1990 (Liukkonen et al. 1997), served as a marker layer for the change in cores. Core B was identical with core A. The uppermost varve (2002) was cut into 8 slices to observe seasonal patterns within the varve (II, IV).

Surface sediments of 31 lakes were sampled using a Limnos gravity corer during the winters of 2003 and 2004. One or two samples were taken from the deepest part of the lake. The uppermost 0–1 cm of sediment (or 0–2 cm in the case of very loose sediments) was used for the analyses. The exact sediment accumulation rate for an individual lake was not known, but it was assumed that the uppermost centimeter represents a time period less than 5 years. The samples were kept frozen at –20 °C in small plastic bags until the analysis of cladoceran remains.

A known volume (1–6 ml, depending on the water content) of fresh, thoroughly mixed sediment from each sample was heated in 100 ml of 10% KOH for 30 min while gently stirring with a glass rod (see Korhola & Rautio 2001; Szeroczyńska & Sarmaja-Korjonen 2007). The samples were then washed on a 50-µm mesh under running tap water. *Lycopodium* spore tablets were dissolved in 10% HCl and mixed with the samples to permit quantitative enumeration of remains. Permanent slides were prepared by dispersing a 50- to 200-µl aqueous suspension of microfossils and using Kaiser's glycerol gelatine, coloured with safranin, as a mounting medium. Remains were enumerated using a microscope with 200x magnification. Identification of the remains was based on Frey (1959), Flössner (1972; 2002) and Szeroczyńska & Sarmaja-Korjonen (2007). The most numerous fragment of each species served to convert the counts into total numbers of individuals according to the formulas of Frey (1986). At least two slides were counted per sample, yielding a total of 319 to 1297 individuals (converted from fragments) per sample. Rotifer eggs were counted along with the cladoceran remains from one or two slides per sample. All, or a maximum of 50 carapaces of each *Bosmina* species were measured for total length (excluding the mucro) from each sample. In 21 surface sediment lakes the maximum number of measured carapaces was reduced to 30.

In Lake Vesijärvi, an additional 4–6 ml of fresh sediment from each layer was heated in 10% KOH and washed on a 100-µm mesh. The whole sample was scanned using an inverted microscope with 100x magnification, and the ephippia of *Daphnia*, *Ceriodaphnia* and *Bosmina* were enumerated and measured (max. 50 of each).

To examine the possible effect of the chosen 50-µm mesh on the results of the exoskeletal remains, the fraction passing through the 50-µm mesh, but remaining on a 25-µm mesh, was studied for the eight samples from core B. A subsample of the remains left on the 25-µm mesh was washed into a plankton cuvette and scanned using an inverted microscope with 200x magnification.

To convert the volume-based concentration of remains to weight units, a known volume (2 to 6 ml) of wet sediment from each sample was analyzed for sediment dry weight (DW) and the organic matter (OM) content. Sediment dry weight was determined after heating at 105 ˚C for 20 h, and the organic content by weight loss on ignition (LOI) at 550 ˚C for 2 h.

3.3 Contemporary data

Most of the contemporary data used in this thesis were extracted from the National database 'Hertta', Lahti Municipal Research Laboratory, the lake monitoring conducted by the University of Helsinki, and from the specific projects described in chapter 3.1. In Lake Vesijärvi, the means of the monthly measurements at a 1-m depth in the open water period were used; except for chlorophyll-*a* and the biomass of cyanobacteria, an integrated sample covering twice the Secchi depth was used (IV, V). Quantitative abundance data on roach and smelt were available for 1984, 1989−1993, 1996 and 2002–2003 (Jurvelius & Sammalkorpi 1995; Peltonen et al. 1999a; Ruuhijärvi et al. 2005; T. Malinen et al. unpubl. data) (V). Zooplankton data were available for 1991, 1993, 1994, 1997, 1999, 2001 and 2002 (Luokkanen 1995; Vakkilainen 2005; Vakkilainen & Kairesalo 2005). Zooplankton sampling and counting methods are described in detail in paper II.

Data collection and sampling methods of the joint Nordic Lake Survey (821 lakes; I) are described in Henriksen et al. (1996; 1997; 1998) and Mannio et al. (2000). The contemporary data for the test sets of lake classification (25 lakes, I) and surface sediments (31 lakes) were gathered from various sources, and sampling methods therefore differed between the lakes. In the ECOFRAME project, water chemistry and phytoplankton samples consisted of pooled tube samples from the nonstratified part of the lake centre, while in other projects the lakes were sampled at the deepest point of the lake separately 1 m below the surface and 1 m above the lake bottom. All 31 surface sediment lakes were additionally sampled for water chemistry on the day of sediment sampling 1 m below the surface and 1 m above the lake bottom at the sediment sampling point. Total phosphorus, total nitrogen, pH, alkalinity and conductivity were analysed using standard laboratory techniques. As a measure of the concentration of humic substances, spectrophotometric light absorbtion at 400 nm was measured in filtered (Whatman GF/C) water against distilled water using 2-cm cuvettes. Absorbances were normalized to a 5 cm path length and converted to a concentration of yellow substances according to a formula provided by the Estonian part of the ECOFRAME project consortium (Nõges Tiina, University of Tartu, personal communication). To harmonize the datasets and to avoid the influence of possibly deoxygenated hypolimnion with distinctive chemical features, only the data on the surface water samples were used. When several relevant measurements were available, mean values were used. All contemporary water chemistry data used were measured 0–6 years before sediment sampling.

Each surface sediment lake was fished using Nordic multimesh gillnets (Böhling & Rahikainen 1999) during the projects specified in chapter 3.1. The number of gillnet nights ranged from 4 to 52, depending on the lake size. Fishing effort per lake area varied from 0.03 to 2.22 nets ha^{-1}. In all lakes, fishing was conducted within 5 years before the sediment sampling. Fish species were arranged into three feeding guilds, although some species are rather omnivorous (roach, *Rutilus rutilus* (L.)), or switch diets during their lifespan (perch, *Perca fluviatilis* L.). The feeding guilds were planktivorous fish (smelt *Osmerus eperlanus* (L.), vendace *Coregonus albula* (L.), whitefish *Coregonus lavaretus* (L.), bleak *Alburnus alburnus* (L.), roach and perch <10 cm), benthivorous fish (ruffe *Gymnocephalus cernuus* (L.), bream *Abramis brama* (L.), white bream *Blicca bjoerkna* (L.), rudd *Scardinius erythrophtalmus* (L.), ide *Leuciscus idus* (L.), tench *Tinca tinca* (L.), crucian carp, *Carassius carassius* (L.), bullhead *Cottus gobio* L. and perch 10–15 cm), and piscivorous fish (pike *Esox lucius* L., pikeperch *Stizostedion lucioperca* (L.), burbot *Lota lota* (L.), asp *Aspius aspius* (L.) and perch >15 cm).

3.4 Data analysis

Spearman rank correlation analysis was used in several cases: 1) to explore relationships among the numerical variables used in the ecological classification of 25 lakes and the ‘expert judgement’ concerning the lake quality status (I); 2) to determine in which unit species data should be expressed to achieve the best correlation between the annual subfossil data and plankton data in Lake Vesijärvi (II); 3) to test whether the abundance of rotifer eggs in Lake Vesijärvi sediment correlated annually with the total phosphorus or chlorophyll-*a* concentration in the water column (IV) and, finally; 4) to test whether the concentrations of different species remains (expressed as No. g^{-1}OM) in 31 surface sediment lakes correlated with the sediment organic matter content (LOI%).

Differences in the mean size of cladoceran ephippia among the annual laminations of lake sediment were tested for significance with one-way analysis of variance (ANOVA), followed by a post hoc Tukey HSD test for multiple comparisons. In the case of heterogeneous variances (Levene test $p > 0.05$), the non-parametric Kruskal-Wallis test was used (III). The Kruskal-Wallis test, followed by non-parametric multiple comparisons (Conover 1980), was also used to test the statistical significance of species-specific differences in the annual net accumulation of remains in the sediment in relation to the calculated exuviae production in the water column (II). Exuviae production was calculated for each pelagic species, using cladoceran densities and water temperatures separately from the epi- and hypolimnion. Together with formulae for egg turnover times from the literature (Vijverberg 1980), moulting rates per individual per day were estimated, and extended over the growing season (Kerfoot 1981; 1995; more details in paper II). Finally, the Kruskal-Wallis test, followed by non-parametric multiple comparisons (Conover 1980), was used to examine the statistical significance of changes between the four time periods, specified by changing fish abundance (more details in paper V). The tested variables included the mean sizes of ephippia and carapaces, species abundances, various indices based on cladoceran remains, as well as contemporary water quality parameters and meteorological data.

The Wilcoxon signed-rank test was used to test the reproducibility of cladoceran analysis, by comparing species abundances in the same varve of two separate cores (A and B) in Lake Vesijärvi (II).

The rate of change, an estimate of the amount of change per unit time (Jacobson & Grimm 1986), was assessed by calculating a chord distance between adjacent samples of Lake Vesijärvi sediment, in which species abundances were expressed as percentages (V).

Multivariate ordination analyses were used both in Lake Vesijärvi and in the set of 31 lakes. Detrended correspondence analysis (DCA; Hill & Gauch 1980), with detrending by segments and non-linear rescaling of axes, was used to determine the gradient length for the first axis. In the case of a short gradient length of species compositional turnover along the first DCA axis (S.D. < 1.5), principal component analysis (PCA) was selected as an appropriate unconstrained ordination, and redundancy analysis (RDA) as a constrained ordination for the data (ter Braak & Prentice 1988).

Concurrent yearly species assemblages in the sediment and in the plankton of Lake Vesijärvi were compared using standardized PCA (II). Percentage abundance data were square-root transformed prior to analysis. The same method, but with subfossil zooplankton expressed as absolute abundances (No. g^{-1}OM), was used to explore the annual changes in the community composition over the whole study period in Lake Vesijärvi (V).

Multivariate constrained ordination was used for the additional data set of 31 lakes presented in this thesis. Prior to statistical analysis, environmental variables were transformed to approximate a normal distribution (Table 1). Redundancy (collinearity) among the environmental variables was explored by standardized PCA and by variance inflation factors (VIF). Variables with VIF > 20 (i.e. multiple collinear variables that have no unique contribution to the regression equation; ter Braak & Šmilauer 2002) were removed one at a time, until all variance inflation factors were < 20. Species data were expressed as log(x+1)-transformed absolute abundances (No. g^{-1}OM). RDA was applied to examine the relationship between the species data and environmental variables (ter Braak & Šmilauer 2002). To estimate the contribution of explanatory power for each variable, a series of RDA ordinations was run, taking only one environmental variable at a time and the remainder as covariables (partial RDA; ter Braak 1995; ter Braak & Šmilauer 2002). The Monte Carlo permutation procedure (499 iterations) was used to investigate the statistical significance of the effects of each variable. Finally, the environmental data were divided into three components: physical (max. depth, mean depth, surface area, LOI%), chemical (total N, total P, pH, conductivity, colour, Secchi depth) and a fish component (fish size and BCPUE of planktivorous, benthivorous and piscivorous fish). Variance partitioning was applied to determine how variation in the species response is partitioned according to these three components (Borcard et al. 1992).

Finally, the responses of various subfossil-based indices to re-oligotrophication and fish reduction in Lake Vesijärvi were tested for wider generality with a surface sediment data set of 31 lakes using (multiple) linear regression analysis. As no information on submerged plants was available for the lake set, the Secchi/mean depth was used as a surrogate for the light exposure to the sediment, and thus the potential benthic production (cf. Bjerring et al. 2009). In the case of a skewed distribution (Shapiro-Wilk test of normality, $p < 0.05$), logarithmic or squareroot transformation was applied to normalize the distribution of variables prior to analysis.

Software used for the analysis included SPSS 15.0, PC-ord 4.20 (McCune & Mefford 1999) and CANOCO version 4.53 (ter Braak & Šmilauer 2002).

3.5 Taxonomic remarks

The taxonomy of cladocerans is undergoing change, as new species are being found and old species are being redefined. The old paradigm of cosmopolitanism in the biogeography of cladocerans has been replaced by non-cosmopolitanism or continental endemism (Frey 1987; Korovchinsky 1996; Belyaeva & Taylor 2009). Recent studies combining sexual stage morphology with molecular methods have, for instance, improved the taxonomy of the genus *Bosmina* (Kotov et al. 2009), led to definitions of new genera from the diverse genus *Alona* (Van Damme et al. 2009), and revealed cryptic species within the *Chydorus sphaericus* species complex (Belyaeva & Taylor 2009).

The taxonomy of Bosminidae has been extremely controversial (Kotov et al. 2009). A good example of the situation was the latest version of Flössner's (2000) comprehensive book on cladocerans in Europe, from which the author left this family out. Controversy has existed over whether different morphotypes represent real evolutionary lineages or merely polymorphism (cf. Haney & Taylor 2003). The morphological features used for identification (size and shape of carapace, antennules and mucro) show marked seasonal changes and phenotypic plasticity attributed to predation (Lagergren & Stenson 2000). These ecologically plastic characters seem to have a genetic component, however (Kerfoot 2006). Recent, detailed multipopulation studies by Faustová et al. (2010; 2011) using subfossil, morphometric and genetic material have provided evidence that several species radiated from *Bosmina (E.) longispina* during Holocene, and that *Eubosmina* morphotypes in Europe represent a group of young species undergoing speciation with apparent reproductive barriers, although some intermediate forms also exist. Their results supported the taxonomy of Lieder (1996), with four species and eleven subspecies of *Eubosmina* in Europe, namely *B. (E.) longispina, B. (E.) coregoni, B. (E.) crassicornis* and *B. (E.) longicornis.* Therefore, this nomenclature is used in the synopsis of this thesis.

The nomenclature used for *Bosmina (E.) crassicornis* in Lake Vesijärvi varies between papers II–V, as well as in previous publications on Lake Vesijärvi

(*Bosmina crassicornis* in Horppila 1997; Kairesalo et al. 1999; *Bosmina coregoni* in Luokkanen 1995; Sammalkorpi 1995; Horppila et al. 2000; Vakkilainen & Kairesalo 2005). In II and III, the species was called *Bosmina coregoni,* but in the last paper (V), the name was updated to *Eubosmina crassicornis*. In Lake Vesijärvi sediment, this morphotype was relatively easy to determine. Generally, however, it is often difficult to accurately identify species within the subgenus *Eubosmina* from detached body parts, especially when several species coexist (Szeroczyńska & Sarmaja-Korjonen 2007). The surface sediment samples presented in this thesis were diverse, including *B. (B.) longirostris, B. (E.) longispina* as well as *B. (E.) crassicornis, B. (E.) coregoni, B. (E.) longicornis,* and possibly some intermediate forms or subspecies. The observed diversity of *Bosmina* species in the sampling area was in accordance with the provisional list of cladocerans in Finnish biogeographical provinces (Silfverberg 1999). In the data analysis of surface sediment samples I distinguished *B. (B.) longirostris, B. (E.) longispina* and *B. (E.)* cf. *coregoni*, to which I included *B. (E.) coregoni, B. (E.) crassicornis, B. (E.) longicornis* and their possible subspecies or intermediates.

The status of *Eubosmina* Seligo 1900 as a genus or as a subgenus differs in the literature as well as in the taxonomical databases of ITIS (Integrated Taxonomic Information System) and Fauna Europeae. In paper V, ITIS was followed, because of a more recent update at that time (Taylor et al. 2002). Recently, however, Kotov et al. (2009) recommended the single-genus approach because of weak morphological differentiation among subgenera.

Species found in the sediment samples of Lake Vesijärvi are listed in paper V. Species found in the set of 31 lakes are presented in Figure 4 with the frequencies of observations. Species were

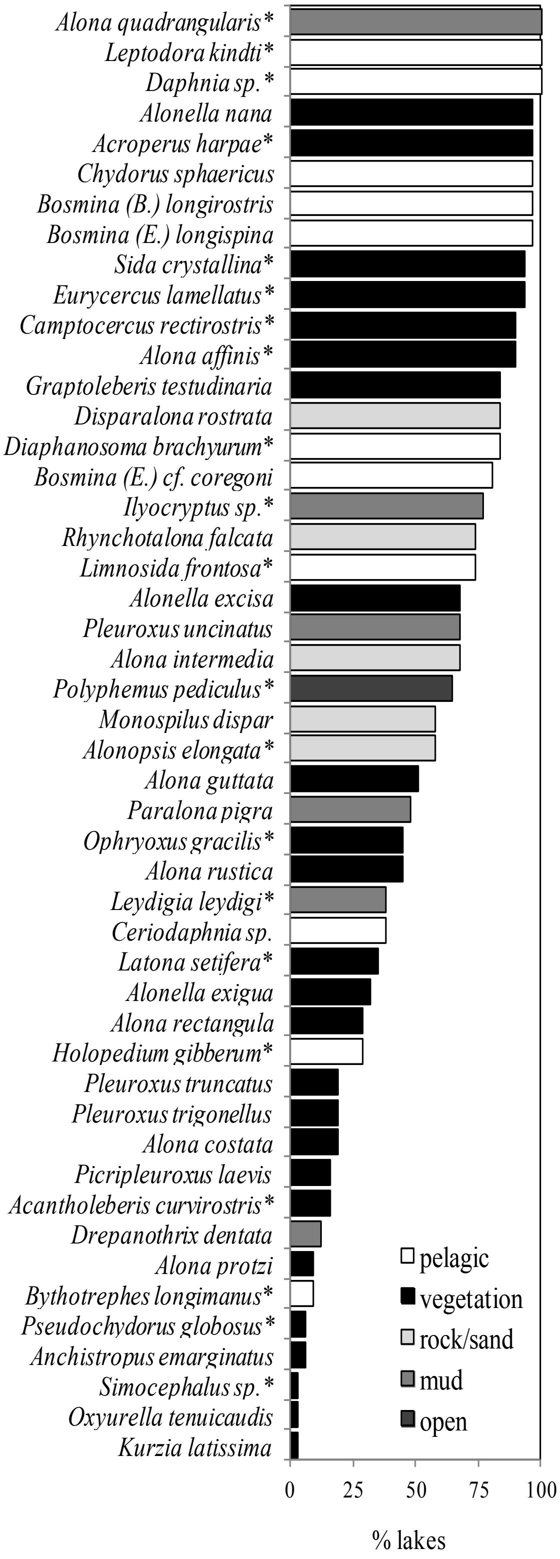

Figure 4. Frequencies of taxa observations in the 31 lakes in southern Finland. Taxa were divided into five groups according to their preferred habitat. Species regarded as large-sized (>0.5 mm) are marked with an asterisk.

divided into five groups in relation to their preferred habitat (pelagic, littoral open water, plant-, rock-, or mud-associated) according to Whiteside & Swindoll (1988), Hann (1989), Flößner (2000), and zooplankton monitoring results from Lake Vesijärvi. Another grouping of species was formed on the basis of their size, comprising small (<0.5 mm) and large (>0.5 mm) species, according to the size ranges reported by Flößner (1972; 2000). In data analysis, pelagic species were treated at the species level and littoral species as species groups according to their preferred habitat.

4. RESULTS AND DISCUSSION

4.1 Taphonomy of cladoceran remains

Poorly preserved species

The deposition of remains in Lake Vesijärvi sediment differed significantly among pelagic cladoceran species. The differences were revealed by a comparison of the annual net accumulation of remains in deepwater sediment with the calculated summertime exuviae production in a vertical column of water above the deepest point (II). The accumulation of remains was similar to or exceeded the expected values for species regarded as well preserved (all *Bosmina* species, *Chydorus sphaericus*), while only a fraction of expected production was recovered from the sediment for species regarded as poorly preserved (*Daphnia* sp.*,* *Ceriodaphnia* sp. and *Diaphanosoma brachyurum*; Frey 1986; Hofmann 1987). Much of this difference was explained, however, by sample preparation with a sieve. Owing to the poor preservation of carapaces, counts for these species are based on small claws and exopodites. The majority of *Daphnia* claws (87%), *Diaphanosoma* exopodites (63%), and even some *Limnosida frontosa* claws (21%), passed through the 50-µm sieve when studied from the uppermost varve. The claws of *Ceriodaphnia* were entirely lost (II).

The effect of sample preparation on the results is rarely considered. Typically, samples are heated in 10% KOH and then sieved (Hann 1989; Korhola & Rautio 2001). Additional chemical treatment with acids may be used for inorganic sediments (Frey 1986), but is not recommended, as it may cause further dissolution of remains (Korhola & Rautio 2001). Matveev (1986) reported, however, that the normal procedure with heating in KOH led to considerable losses of *Daphnia* remains, while *Bosmina* carapaces were more resistant. The most commonly used mesh sizes in cladoceran analysis range from 37 to 55 µm (Frey 1986; Hann 1989; Korhola & Rautio 2001), but 63-µm (Hauptfleisch et al. 2010) or 80-µm meshes are also used (e.g. Jeppesen et al. 1996; Amsinck et al. 2006; Bjerring et al. 2008). A mesh size >100 µm is only used for infrequent remains, such as ephippia (e.g. Verschuren & Marnell 1997; Jeppesen et al. 2002; Davidson et al. 2010a). Uncertain retention or preservation of *Daphnia* and *Ceriodaphnia* claws have led some researchers to count only sexually produced ephippia (e.g. Verschuren & Marnell 1997; Jeppesen et al. 1996; 2002; 2003b; this study in the case of *Ceriodaphnia*), even though the abundance of ephippia may not reflect the size of the parthenogenetic population (e.g. Frey 1982; Jankowski & Straile 2003; Keller & Spaak 2004). The selection of mesh size depends on the purpose of the study, but it may also be dictated by practical constrains, when dense mesh retains silty sediment obscuring the remains (cf. Verschuren & Marnell 1997).

The preservation of *Daphnia* remains is highly selective. Besides ephippia and postabdominal claws, mandibles and variably preserved tail spines or shell margins can also be found, especially in surface sediments (Sarmaja-Korjonen 2007). On rare occasions, headshields have been reported (Frey 1991; Manca et al. 1999; Manca & Comoli 2004; Szeroczyńska & Zawisza 2005). The retention of different daphnid remains varied both in Lake Vesijärvi sediment and in surface sediment from the set of 31 study lakes (Fig. 5). On a 50-µm sieve, daphnid claws and mandibles were quite equally represented, while shell margins and tail spines were usually more abundant, but also more variable among the lakes. Sarmaja-Korjonen (2007) found more tail spines than claws in the surface sediments of 10 out of 17 lakes in central and southern Finland, when using a 44-µm mesh. She suspected that the differences among the lakes were related to water chemistry. Leavitt et al. (1993) observed fragmentation of shell margins and the disappearence of tail spines in fish stomachs, adding consumption by fish as an additional source of variation among lakes. They also observed a light colour in moulted claws, and dark claws in dying *Daphnia*. According to Frey (1986), the first few instars of cladocerans are poorly preserved. In Lake Vesijärvi sediment, a light color and visible signs of dissolution of *Daphnia* claws and *Diaphanosoma* exopodites, especially in the fraction passing through the 50-µm sieve, could imply that the smallest remains passing through the sieve were from early moults.

To what extent is the preservation of zooplankton remains a lake-specific feature? Decomposition depends on mechanical, chemical and biological processes (Kerfoot 1995), which vary within and between lakes. In deep lakes, remains may stay longer in the water column before reaching the sediment surface, while in shallow lakes remains may resuspend several times from oxidated sediments before final burial. Jeppesen et al. (2002) suspected that the poor preservation of daphnid remains they observed in shallow lakes was due to frequent resuspension.

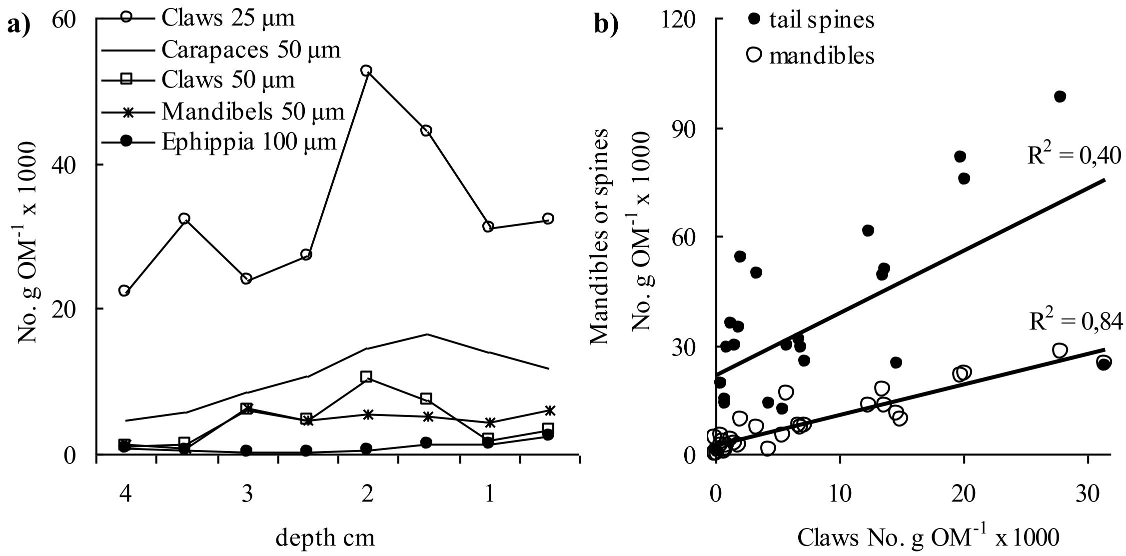

Figure 5. a) Concentration of various remains of *Daphnia* within the uppermost annual varve of sediment in Lake Vesijärvi. Mesh sizes used are indicated in the legend. **b)** The abundance of mandibles and tail spines in relation to claws in the surface sediments of 31 lakes in southern Finland, using a 50-µm mesh.

The sediment organic content (LOI%) might serve as an indicator of sedimentary conditions in a lake, although the interpretation is not straightforward. The sediment organic content is favoured by increasing lake productivity, reduced conditions in the sediments slowing down the degradation of organic material, influxes of terrestrial or littoral organic matter, as well as by organic anthropogeneous discharges (Håkanson & Jansson 1983). Conversely, the sediment accumulation rate, enhanced by resuspension and erosional allochthonous fluxes, correlates negatively with organic content. Thus, the total number of cladoceran remains expressed per unit dry weight of sediment is generally higher in organic than in minerogenic sediments (Korhola & Rautio 2001). The number of remains expressed per unit weight of organic material, however, should partially correct for between-lake differences in the trophic state and sediment accumulation rate (Verschuren & Marnell 1997).

When the concentrations of species (ind. [g OM]$^{-1}$) in a set of 31 lakes were related to LOI%, all the species considered as poorly preserved showed a significant positive correlation with LOI%: *Daphnia* claws/mandibles ($r_s = 0.645$, $p < 0.001$), *Diaphanosoma* exopodites ($r_s = 0.377$, $p = 0.036$), *Ceriodaphnia* claws ($r_s = 0.414$, $p = 0.021$) and *Holopedium* postabdomes ($r_s = 0.629$, $p < 0.001$). Other species that correlated positively with LOI% were *Bosmina (E.) longispina* ($r_s = 0.649$, $p < 0.001$), plant-associated species ($r_s = 0.683$, $p < 0.001$) and rotifer eggs ($r_s = 0.425$, $p = 0.017$). LOI% was significantly correlated with several environmental variables, for instance, negatively with TP and conductivity (Table 2). This hampers direct interpretation. *Bosmina (E.) longispina* is known to prefer oligotrophic, low conductivity lakes (Boucherle & Züllig 1983; Hofmann 1987). The weak positive correlation between LOI% and the Secchi/mean depth (a surrogate for submerged vegetation) might explain the positive correlation between plant-associated species and LOI%. There is no information on whether rotifer resting eggs are better preserved in organic sediments. One possibility, however, is that a high organic content contributes to the better extraction of small remains in sample preparation, because the need for rinsing is considerably less for organic sediments (personal observation). The significant, positive correlation with LOI% of all the species generally regarded as poorly preserved (i.e. *Daphnia, Diaphanosoma, Ceriodaphnia* and *Holopedium*; Deevey 1964; Frey 1986; Hofmann 1987; Rautio et al. 2000) may indicate, however, that they were better preserved in lakes with organic sediments. Pigments, for example, are known to be better preserved in sediments rich in organic matter (Sanger 1988). Nevalainen (2007) found well-preserved *Ceriodaphnia* claws and postabdomens in small, *Sphagnum*-dominated bog ponds, where highly organic sediment probably enhanced their preservation. These remains are sometimes completely lost. Rautio et al. (2000) observed *Holopedium* in plankton samples and in sediment traps in Lake Saanajärvi, but did not find any remains in the sediment. Davidson et al. (2007) did not find remains of *Diaphanosoma* in a set of 39 UK and Danish lakes, although the species was present in contemporary samples.

Overall, the method for sample preparation used in this study was highly reproducible, as the counts from two parallel cores in Lake Vesijärvi yielded similar result (Fig. 2 in II). The obvious effect of sieving, however, stresses the importance of using the same method for all samples being compared, for example, when inferring lake history by applying transfer functions (e.g. Jeppesen et al. 1996), multiple regression trees

(Davidson et al. 2010a,b) or other models derived from surface sediment data sets. More studies are needed to clarify lake-specific differences in the preservation of cladoceran remains. For example, diatom preservation is known to decline with increasing pH, temperature, coarseness of the sediment, grazing and bioturbation, water depth and exposure. Meanwhile, preservation is aided by diatom robustness, the sediment accumulation rate and diatom concentration (Flower 1993).

Well-preserved species

In Lake Vesijärvi the accumulation to production ratios for well-preserved species showed differences that were more likely to be attributable to sediment transportation processes than to differences in preservation, especially when the accumulation exceeded the expected production. The accumulation to production ratio was two-fold higher for epilimnetic species (*Bosmina (E.) crassicornis* and *Chydorus sphaericus,* medians 2.4 and 2.3) than for the species mainly inhabiting the hypolimnion (*Bosmina longirostris* and *Bosmina (E.) longispina,* medians 1.0 and 0.9, respectively). The difference between epi- and hypolimnetic species fits notably well with the relative volumes of epi- and hypolimnion in the lake, which have a ratio of 2:1 with a depth boundary of 10 m. Therefore, not only vertical fluxes, but also horizontal fluxes contributed to the accumulation of remains in the deepest point of the basin. The importance of horizontal fluxes was even more clearly seen for those epilimnetic species that occurred at low densities above the deepest point. High ratios of accumulation to production in the case of epilimnetic *Limnosida frontosa* (median 5.5) and *Leptodora kindtii* (median 22.0) indicated that the majority of their remains came from shallower pelagial areas where *Leptodora*, at least, is known to be more abundant (T. Saarinen, unpublished Master's thesis). Interestingly, Alajärvi and Horppila (2004) observed a significant increase in the abundance of both *Leptodora* and *Limnosida* during the night in Lake Hiidenvesi, Finland, indicating horizontal movements towards the open water at night. Thus, according to sediment data, these species are more abundant in Lake Vesijärvi than expected from the single station daytime monitoring of zooplankton, which may additionally underestimate large species because of their potential ability to avoid the sampling device (de Bernardi 1984).

The high accumulation to production ratios are in accordance with the high sediment resuspension rate known to occur in Lake Vesijärvi, which significantly contributes to the gross sedimentation rate in the deepwater area (Liukkonen et al. 1993). According to Koski-Vähälä et al. (2000), as much as 56 to 99% of the gross sedimentation rate was accounted for by resuspended material in 1993 and 1994. Although redeposited materials greatly increase the sediment accumulation rate in the deepwater area, the phenomenon seems not to destroy the chronology, as even the seasonal succession of cladocerans (Fig. 5 in II) and diatoms (Liukkonen et al. 1993; 1997; 2006) is preserved within the sediment. High annual variation in the calculated accumulation to production ratio of cladoceran remains (Table 4 in II) may imply, however, that resuspension and sediment focusing efficiency varied between the years. Resuspension can reduce the chronostratigraphic value of sediment, even in the case of annual lamination (cf. Mieszczankin & Noryśkiewicz 2000). However, variations in the ratio caused by inaccurances in sediment dating, in zooplankton sampling giving only snapshots of the true populations or, possibly, in the calculation of exuviae production, neglecting e.g. the effect of food on development times, cannot be ruled out.

The sediment focusing efficiency is a lake-specific phenomenon and connected to lake morphometry (Lehman 1975; Hilton et al. 1986; Blais & Kalff 1995). Although several authors have compared plankton samples with surface sediment or trap samples (e.g. Leavitt et al. 1993; Rautio et al. 2000; Kattel et al. 2007), similar studies quantifying the relationship between the production of remains and their deposition are rare. Kerfoot (1981, 1995) applied a model derived from moulting and death rates, and compared the predicted seasonal vertical flux of *Bosmina* remains with the flux of remains in sediment traps in Lake Washington (Kerfoot 1995). The expected production and observed trap catch strongly correlated, but the absolute catches were considerably less than those found in this study, suggesting that only 4 to 6% of *Bosmina* remains were preserved. Because these values were determined using sediment traps, the results could imply major degradation already occurring in the water column. Lower values can partly be explained by the methods, because unlike in this study, Kerfoot (1995) added death rates to the production of remains, and did not include fragmented remains in the sediment counts. In Lake Vesijärvi, however, inputs of re-sedimented material may counteract degradation losses, whilst in Lake Washington horizontal fluxes were small. Hall and Yan (1997) calculated the annual population growth of *Bythotrephes* after invasion in Harp Lake, Ontario, using spatial distribution and the rate of accumulation of its remains in the sediment. They found only minor dissolution of remains when using a temperature-dependent growth model for the plankton data. Their result was not affected by horizontal fluxes, because the estimate was based on sediment samples from the whole lake area.

Kattel (2009) attempted to quantify species-specific differences in preservation by comparing sediment trap samples to a core-top sample in a small mountain lake in Scotland. The method focused on degradation at the sediment-water interface, and neglected degradation during sinking or in the sediment traps. Kattel's results indicated poor preservation rates for *Daphnia* (5%) and *Ceriodaphnia* (0%), and high or moderate preservation rates for *Bosmina (E.) coregoni* (82%) and *Bosmina (E.) longispina* (59%). The results also suggested differential preservation among littoral chydorid species. The applicability of a pelagial sediment trap as a reference for littoral remains may be questionable, however, as the representation of littoral species assemblages in the lake centre is greatly affected by transport processes from source communities (Kattel et al. 2007). Ultimately, reliable estimates of the degradation rates would probably require an experimental approach (cf. laboratory experiment of Hall & Yan 1997 with *Bythotrephes*).

Importance of units

There are several methods to present data, each having both strengths and weaknesses (Brugam & Speziale 1983). Species given as percentages are independent of the sedimentation rate of the matrix, but the abundances are relative, i.e. they are not independent of each other. Abundances expressed as concentrations are independent of each other, but dependent on the changes in the accumulation rate of the sediment matrix. This dependence is removed when calculating influxes, i.e. the net accumulation of remains. This unit is, however, highly susceptile to variations in sediment focusing, i.e. in the sedimentation pattern of the whole lake, especially when measured as single-core estimates (Lehman 1975; Anderson et al. 1994).

In Lake Vesijärvi the plankton and sediment counts of cladocerans from 7 years, expressed in different abundance units, gave rather similar correlation coefficients (r_s = 0.49–0.55), although correlations in all units were notably stronger if only well-preserved taxa were considered (r_s = 0.80–0.91) (Table 2 in II). The sediment composition was relatively uniform during the study period, explaining the small differences between various concentration units (Fig. 6). The high water content in the sediment surface reduced the concentrations of remains expressed per unit volume of wet sediment (no. ml^{-1}). The high mineral content in the varve from 1991, resulting from dredging of the boat harbour in the previous autumn (Liukkonen et al. 1993), reduced the concentrations of remains in every unit, most obviously when expressed per unit weight of dry sediment. However, in a longer time series from Lake Vesijärvi it became clear that the accumulation rate showed different patterns from the concentration units (Fig. 5 in V; Fig 6).

All concentration units showed a peak in total cladoceran abundance in 1994, just after the biomanipulation. During that time the ratio of chlorophyll-a to total phosphorus was at the lowest level, indicating efficient grazing (Fig. 6; Carpenter et al. 1985; Mazumder 1994). This peak was not as obvious in the accumulation rate as in the concentration units, and not observed in the plankton data (Luokkanen 1995; Fig. 3 in II). In general, the accumulation rate of remains decreased along with a decreasing nutrient status. A similar decrease could not be seen in concentrations. This difference could be explained if the decreased productivity, seen as reduced concentrations of nutrients, chl-a, cyanobacteria and turbidity (Fig. 1 in V), led to an overall decrease in the accumulation rate of the sediment matrix,

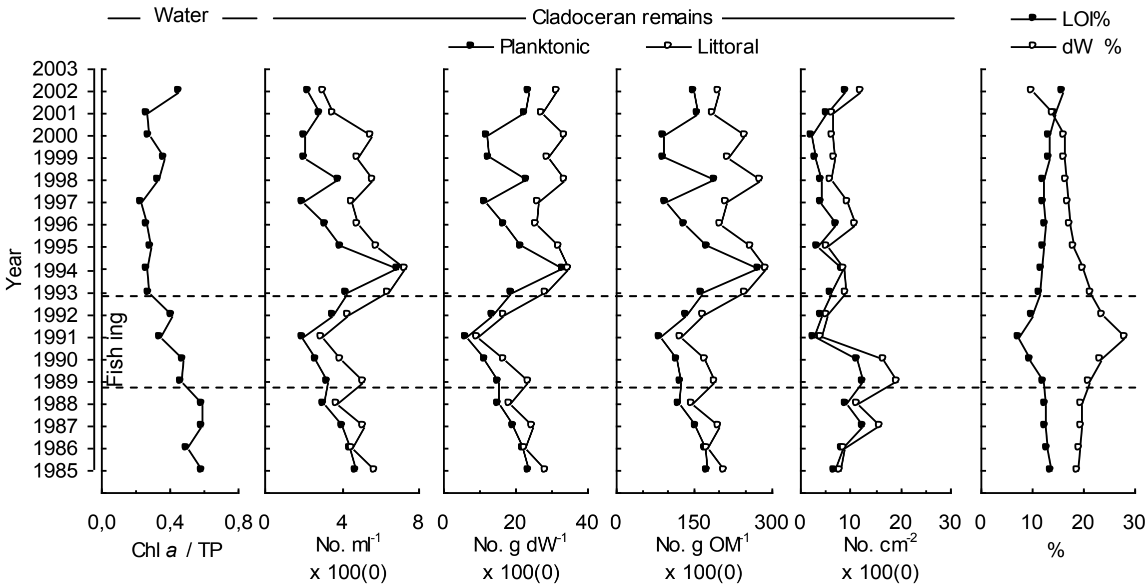

Figure 6. The total abundance of cladoceran remains in Lake Vesijärvi sediment expressed per unit volume of wet sediment (no. ml^{-1}), unit weight of dry sediment (no. g dW^{-1}), unit weight of organic matter (no. g OM^{-1}), and as the annual net accumulation per unit area (no. cm^{-2}). The scale for planktonic species is in thousands and for littoral species in hundreds. The final graph shows the sediment organic content (LOI%) and dry weight %. The first graph shows the ratio of chlorophyll-a to total phosphorus (TP) in the water samples during May–September.

i.e. constituents other than cladocerans. In this case, the apparent concentration of cladoceran remains was not affected or even increased. The other possibility is that the resuspension rate and the efficiency of sediment focusing towards the deepwater area decreased, for instance, because of a lesser amount of wind (Fig. 1 and Table 2 in V), or the expansion of submerged macrophytes to greater depths possibly reduced the resuspension rate. This phenomenon should affect the accumulation rate more than it affects the concentrations of remains (Battarbee 1978). No long-term data were available on the annual changes in sediment redistribution, but the calculations of Koski-Vähälä et al. (2000) from 1993 and 1994 imply that annual differences in sediment redistribution can be high. This interpretation is further supported by the similarity of the net accumulation rate for several planktonic species, littoral species (Fig. 6) and rotifer eggs (IV). Mueller (1964; cited in Frey 1986) found a peak abundance of planktonic species in the depth corresponding to the upper part of hypolimnion. Any changes in the position of this type of concentration zone, or abrupt turbidity currents towards the deepwater area, may affect the concentrations of remains without real changes in productivity. This interpretation in supported by the similarity of the concentrations of several planktonic species and mud-associated species, including the peak concentration in 1994 (Fig. 6 in V).

Other authors have also found discrepancies between accumulation and concentration units. Brugam & Speziale (1983) observed a general increase in the influx of all remains in Lake Harriet, Minnesota, but no increase in the dry weight based concentration. As the influxes of other sediment constituents also increased, the authors argued that the increased net accumulation of remains per se was not linked to the production of cladocerans. Studying the annually laminated sediment of a small headwater lake in the Experimental Lakes Area, Ontario, Hann et al. (1994) reported that the annual ice-free standing stock of *Bosmina longirostris* correlated significantly with the subfossil concentration, but not with the annual accumulation rate. They concluded that this might have resulted from difficulty in accurately estimating the bulk sediment accumulation rate, and advocated further research on the relative accuracy of concentration- and accumulation-based estimates of subfossil abundance. In Lake Vesijärvi, both the concentration and accumulation of remains in the sediment varied several-fold over the years, although zooplankton monitoring results suggested a relatively consistent zooplankton density in Lake Vesijärvi among the 7 years studied (Fig. 3 in II). The lack of zooplankton data from the premanipulation years limits the comparison to only those years when the net accumulation rate was already reduced.

The accumulation rate and concentration of remains clearly revealed different aspects of the sedimentation of cladoceran remains in Lake Vesijärvi. Nevertheless, compositional changes showed similar patterns to plankton data, despite the underrepresentation of certain taxa (Fig. 4 in II). The correlation of percentage abundances of well-preserved species with plankton data was strong (r_s = 0.91, p < 0.001), but also significant when including poorly preserved species (r_s = 0.54, p < 0.001; Table 2 in II). The correlation was weaker than in the annually laminated sediment of Tuesday Lake, where Leavitt et al. (1994) recorded a strong relationship (r^2 = 0.52) between the percentage abundances of species, including poorly preserved species, such as *Holopedium gibberum*. In Lake Vesijärvi, however, no large changes in species composition occurred during the years of comparison. Minor changes in species abundances are easily masked by interannual variation in error sources. Overall, the interpretation of changes in cladoceran communities clearly requires the inspection of results expressed in concentration units, accumulation rates and percentages.

4.2 Community changes along a trophic gradient

Pelagic species composition

Lake Vesijärvi has been used as an example of successful restoration with a combination of biomanipulation and reduction of the external nutrient load (Hansson et al. 1998; Wetzel 2001). The reduced recycling of nutrients from benthic to pelagic habitats by fish was considered as a major reason for the observed recovery after effective fishing in 1989–1993, while the role of zooplankton remained less clear and was considered minor (Horppila & Kairesalo 1992; Luokkanen 1995; Horppila *et al.* 1998). The analysis of cladoceran remains in the varved sediment of Lake Vesijärvi revealed that the pelagic zooplankton community responded to the decreased fish density in a way that was in accordance with the size efficiency hypothesis (Brooks & Dodson 1964; Hall et al. 1976), but the changes were rather subtle (V). The abundance of small-sized rotifers and *Ceriodaphnia* sp. decreased, while large species *Diaphanosoma brachyurum* and *Limnosida frontosa* increased in abundance (V). The relative contribution of *Bosmina (E.) crassicornis* also increased in the period of lowest fish density, while the percentage contribution of the smallest *Bosmina* species, *B. longirostris,* decreased. The slightly elevated fish density and increased turbidity in the late 1990s and early 2000s was also reflected in the community composition, although not all changes were statistically significant. The relative abundance of rotifers, for example, increased again (IV; V). In contrast, no clear changes for the whole study period were observed in the abundance of *Daphnia* sp., *Chydorus sphaericus,* or predatory cladocerans *Leptodora kindtii* and *Bythotrephes longimanus*.

To test the generality of the changes observed in the species composition of Lake Vesijärvi, the set of 31 lakes in southern Finland was subjected to ordination analysis. First, PCA with centering and standardization was run to explore environmental variables. The first two PCA axes accounted for 55.4% of the variation in the environmental data. The primary axis (39.2%) was essentially connected to nutrients, pH, alkalinity and conductivity, while the second axis was connected to water colour and Secchi/mean depth (Fig. 7a). DCA of the species data indicated short gradient length of the first axis (1.048 standard deviation units), and linear ordination methods were therefore applied (ter Braak & Prentice 1988; ter Braak & Šmilauer 2002). In RDA, highly collinear environmental variables were excluded one by one on the basis of their variance inflation factors (alkalinity and Secchi/mean depth; VIF values > 20; ter Braak & Šmilauer 2002). Of the initial 16 variables, 14 were included in RDA. The first two RDA axes explained 45.9% of the total variance in the species data and 67.3% of the variance in the species–environment relationship (Fig. 7c). The first two RDA-axes explained a little less of the total variance in the species data than the first two axes in an unconstrained ordination (56.5%; Fig. 7b), implying that not all important environmental variables influencing cladoceran assemblages were measured. The selected environmental variables were related to the major gradients in the species composition detected by the PCA, however, and were thus useful descriptors of the environmental gradients structuring subfossil assemblages. The interset

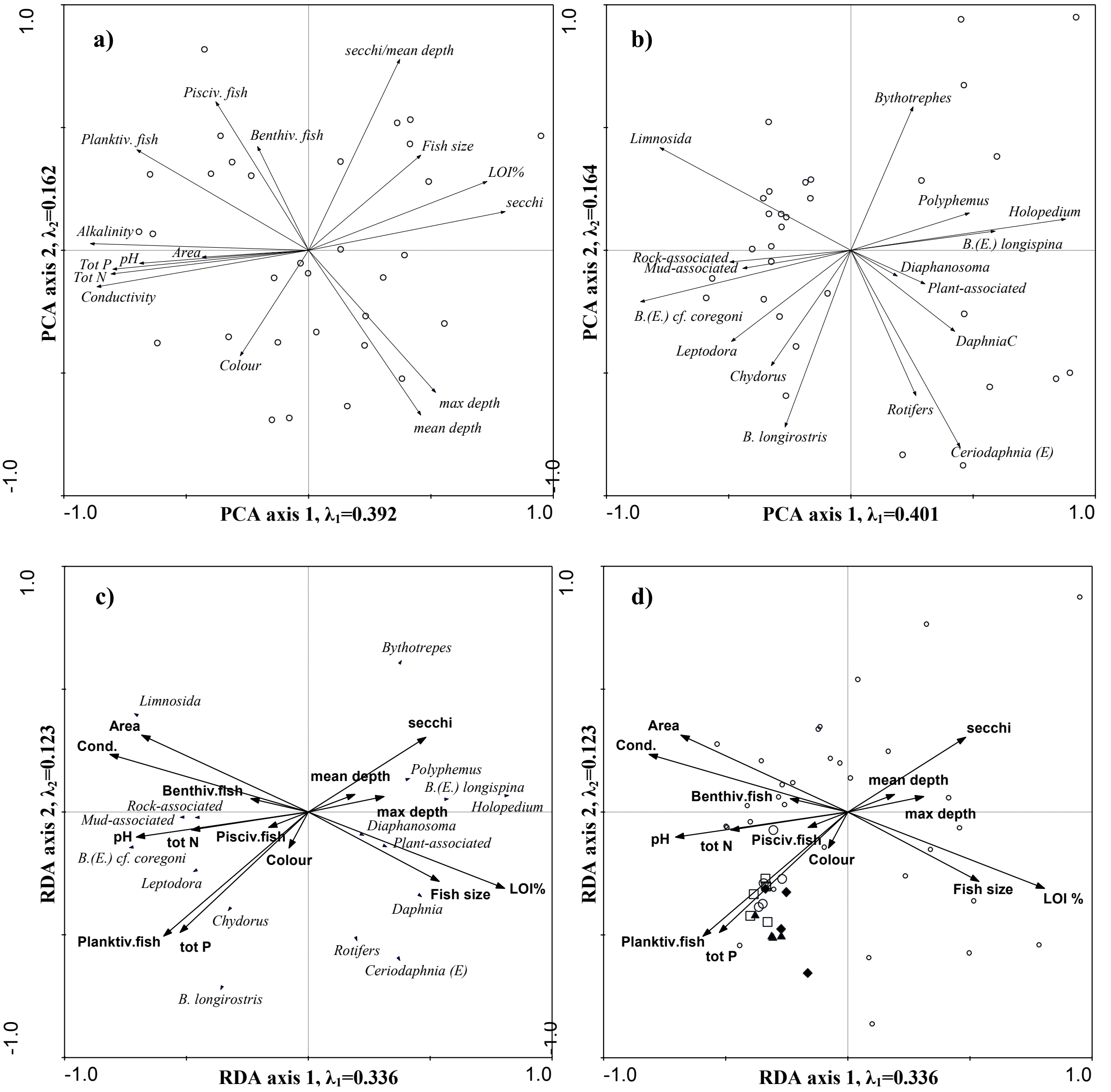

Figure 7. Ordination analysis of the 31 lakes sampled for surface sediments. **a)** PCA of the environmental variables, **b)** PCA of the species data, **c)** RDA biplot showing the relationship between the selected environmental variables and species data, **d)** RDA biplot illustrating the relationship between the environmental variables and sites (small circles). The sediment samples of Lake Vesijärvi (1985-2002) were included in the analysis as passive samples (large symbols): I high planktivorous fish density (black triangles), II fish removal (black diamonds), III low fish density (open squares), IV slightly increased fish density (open circles).

correlations between the environmental variables and the RDA axes indicated a primary axis of conductivity, LOI%, pH and area (Fig. 7c). Total phosphorus and planktivorous fish abundance also correlated with the first axis, but almost equally strongly with the secondary axis.

The subfossil data of Lake Vesijärvi were added post hoc to the RDA ordination by projection, i.e. as passive samples. All the samples were clearly associated in the higher end of the nutrient and planktivory gradients (Fig 7d). The result reinforces the fact that the community changes during re-oligotrophication were rather subtle. Although the total phosphorus concentration decreased in Lake Vesijärvi, it remained above the median value of the 31 lakes (Table 1; the lowest concentration 25.5 µg/l in 1997). Therefore, the subtle changes in the species composition were of the correct scale when compared with the much longer environmental gradient of the surface sediment data set.

In RDA, the species that were positively related to total phosphorus concentration and planktivorous fish density were *Chydorus sphaericus, Bosmina longirostris, Bosmina (E.) cf. coregoni* and *Leptodora kidtii*, all common or even dominant zooplankton species in Lake Vesijärvi (Fig. 7c). *Ceriodaphnia* and rotifers were also positively related to TP. This result deviates from that of Jeppesen et al. (1996), probably because of the difference in the nutrient gradient. In a set of 30 Danish lakes *B. longirostris* and rotifers were positively associated with TP and fish NCPUE, but in contrast, *B. (E.) coregoni* and *Leptodora* showed a unimodal response and were negatively associated with TP and NCPUE in canonical correspondence analysis (CCA). Nutrient concentrations in their lake set were considerably higher than in this study, the lowest TP value (25 µg/l) being close to the median, and the median value (150 µg/l) being well above the maximum of the Finnish lake set (Table 1). Species associated with lower trophy, *Bosmina (E.) longispina, Holopedium gibberum* and *Bythotrephes longimanus,* were rare or nonexistent in their study. The result highlights the importance of locally derived training sets in environmental predictions.

Taken by species, RDA supported the indication value of *Chydorus sphaericus* for eutrophy (Whiteside 1970; de Eyto 2001; Manca et al. 2007). In addition to enriched lakes, *C. sphaericus* is also encountered in littoral zones, small bog waters and in acid lakes (Korhola 1992). Apparently, *Chydorus sphaericus* is a complex of several species (Belyaeva & Taylor 2009), which may explain the observed bimodal distribution regarding pH. The set of 31 lakes included no acid lakes, and the response of *C. sphaericus* to the nutrient gradient was clear. The proliferation of *C. sphaericus* in lake pelagic zones has been connected to cyanobacterial blooms (Flößner 2000). In Lake Vesijärvi, however, *C. sphaericus* remained as a significant part of the pelagic plankton community, and did not decrease along with the biomass of cyanobacteria (Fig. 3 in II; V). Sammalkorpi (1995) has summarized the few, irregular observations of Lake Vesijärvi zooplankton from the early 1900s until the beginning of fish manipulation in 1989. *C. sphaericus* increased in abundance during the eutrophication, being absent in the early 1900s but relatively common in the 1960s. Similarly, in Lake Maggiore, Italy, the abundance of *C. sphaericus* increased greatly during eutrophication, but decreased only slightly during the re-oligotrophication phase (Manca et al. 2007).

There are no historical records of the relative importance of different *Bosmina* species, although *B. (E.) cf. coregoni* has probably always been common in Lake Vesijärvi (Sammalkorpi 1995). During the study period the most abundant species was epilimnetic *B. (E.) crassicornis*, while *B. (E.) longispina,* as well as *B. longirostris* were restricted to the hypolimnion (II). Epilimnetic *B. (E.) crassicornis* was a favoured food of roach (Horppila et al. 2000), and its abundance responded positively to the released predation pressure. The responses of hypolimnetic species were less clear (V). The species replacement of *B. (E.) longispina* by *B. (E.) coregoni* or *B. longirostris* is widely observed in eutrophication (Boucherle & Züllig 1983; Hofmann 1987; Frey 1988; Szeroczyńska

1998; Alliksaar et al. 2005), although the succession may also be related to predatory interactions rather than to the trophic state (Nilssen 1978; Kerfoot 1981). Stenson (1976) compared *B. (E.) coregoni* and *B. longirostris* in fish stomachs and net plankton and showed a clear preference of fish for the larger species, *B. (E.) coregoni*. In hypertrophic lakes, *B. longirostris* survive, but *B. (E) coregoni* seems to disappear (cf. Jeppesen et al. 1996). In oligotrophic waters, however, *B. longirostris* may also coexist with *B. (E.) longispina* (Frey 1988). Lotter et al. (1998) suggested *B. longirostris* as indicative of eutrophic conditions only when it occurs alone or with other eutrophic species, such as *B. (E.) coregoni*. The RDA of 31 lakes supported the general division of *Bosmina* species according to lake trophy. *B. (E.) longispina* was associated with clear-water lakes of low trophy, while *B. (E.) cf. coregoni* was associated with nutrient-rich lakes, and *B. longirostris* with nutrient-rich, shallow, brownwater lakes. It has been hypothesized that eutrophication and predatory interactions are driving forces for a relatively recent speciation of *Bosmina (E.) coregoni, crassicornis,* and *longicornis* in Europe, *B. (E.) longispina* being a parental species (Faustová et al. 2010; 2011). In the RDA *B. (E.) cf. coregoni* and *B. (E.) longispina* were at the opposite ends of the first ordination axis, indicating separate niches. Species-level identification of *Bosmina* remains clearly provides more information on lake ecological quality, or at least the separation of *B. (E.) longispina* from other *Eubosmina.*

Leptodora kindtii associated with nutrient rich lakes in the RDA. In highly eutrophic lakes, *Leptodora* probably decreases in abundance (cf. Jeppesen et al. 1996). Sammalkorpi (1995) did not mention *Leptodora* from old records of Lake Vesijärvi zooplankton, but information is probably lacking because of the small volume of old samples. *Leptodora* may exert heavy predation on herbivorous cladocerans (Branstrator & Lehman 1991) and compensate for the fish predation effects, contributing to the apparent stability of the herbivore community in the course of changing fish predation (Lunte & Luecke 1990). In Lake Vesijärvi, the sedimentary remains of *Leptodora* indicated relatively stable abundance despite fish manipulation (V). The efficient fishing did not reduce the abundance of perch (Peltonen et al. 1999b), however, which favour *Leptodora* in their diet (Horppila et al. 2000).

Sammalkorpi (1995) did not list *Ceriodaphnia* from former records of Lake Vesijärvi zooplankton. In plankton samples from the 1990s, *Ceriodaphnia quadrangula* was not very abundant and was restricted to the hypolimnion (II). *Ceriodaphnia* belongs to microfilterers and efficient bacterial feeders, usually associated with meso- or eutrophic conditions (Geller & Müller 1981; Flößner 2000). The size range of algae used is even smaller than with *Bosmina* (Cyr & Curtis 1999). On the basis of ephippia in the sediment, *Ceriodaphnia* decreased in abundance along with the re-oligotrophication of the lake (V). In the surface sediments of 31 lakes, *Ceriodaphnia* was more frequently found as ephippia than as claws, and was thus included in RDA as ephippia. In RDA the species was associated with higher trophy, but not as clearly as, for instance, *Chydorus sphaericus* and *Bosmina longirostris,* possibly because of its preference for small ponds and littoral zones (Flößner 2000).

The total abundance of rotifers can increase by several orders of magnitude in association with lake eutrophication (Wallace & Snell 1991). According to Sammalkorpi (1995), the total abundance of rotifers, especially of species indicating eutrophy, clearly increased along with the eutrophication of the Enonselkä basin. The accumulation of rotifer eggs in the sediment decreased along with re-oligotrophication, and the ratio of rotifer eggs to the total of cladocerans and rotifers was the lowest in the period of clear water and low fish density (IV, V). In RDA analysis of 31 lakes, rotifers were associated with higher trophy, but not clearly. As mentioned before, the number of eggs was positively correlated with LOI%. In a multiple regression, both LOI% and TP appeared significant in explaining the total abundance of rotifer eggs in the sediment ($r^2 = 0.39$; $p = 0.001$ LOI%$_{sqrt}$, $p = 0.003$ TP$_{log}$). Although LOI% and TP were both also correlated with several other environmental variables (Table 2), the result implies that the total abundance of rotifer eggs was significantly related to TP, although other, possibly taphonomical factors obscured the pattern in this data set.

In addition to *Bosmina (E.) longispina*, species clearly associated with the oligotrophic end in RDA were *Bythotrephes longimanus* and *Holopedium gibberum.* Cotten (1985) studied recent sediments of 46 lakes in eastern Finland and especially found *Holopedium* in deeply coloured, acid lakes. *Holopedium* feed on a narrower size range of algae than large *Daphnia* (Cyr & Curtis 1999). During the experimental manipulations of Tuesday Lake, Wisconsin, *Holopedium* prevailed with *Daphnia pulex* in periods of low planktivorous fish density (Leavitt et al. 1994). In Lake Vesijärvi, *Holopedium* is only occasionally recorded in plankton samples, and no remains of this poorly preserved species were found in the sediment.

Bythotrephes longimanus also only occasionally exists in the plankton samples of Lake Vesijärvi. Based on only a few remains found in the sediment, no conclusions can be drawn on whether this species is increasing in abundance. An increase of this species could have profound effects on the zooplankton. In Lake Maggiore, Italy, *Leptodora* became the dominant predator during eutrophication, but *Bythotrephes longimanus* increased excessively during re-oligotrophication, and exerted heavy predation on cladocerans, leading to a decreased abundance of *Daphnia* and increased abundance of colonial rotifers (Manca & Ruggiu 1998; Manca 2011).

Daphnia sp., *Diaphanosoma brachyurum* and *Limnosida frontosa* were not clearly related to the trophic gradient in RDA, but the first two were closely related to LOI%. As discussed before, taphonomical factors may contribute to the result. There was a significant positive relationship between LOI%$_{sqrt}$ and both the abundance of *Daphnia*$_{log}$ ($r^2 = 0.33$, $p = 0.001$) and *Diaphanosoma*$_{sqrt}$ ($r^2 = 0.16$, $p = 0.024$). Adding TP$_{log}$ as an independent variable to the regression did not explain any additional variance in either case ($p > 0.05$). *Diaphanosoma* thrives in acid conditions (Nilssen & Sandøy 1990), humic waters (Cotten 1985), and among vegetation (Flössner 2000; Declerck et al. 2007) in overgrown lakes and nutrient-poor mire pools (Korhola 1992). It is a microfilterer and efficient bacterial feeder, usually associated with oligo-mesotrophic conditions (Geller & Müller 1981; Flößner 2000), and is known to disappear in heavy eutrophication (Flößner 2000; Stich 2004). It is also regarded as a warmwater species (Herzig 1984). The increase in *Diaphanosoma* in Lake Vesijärvi during re-oligotrophication was in accordance with observations from some other lakes. In Lake Constance, *Diaphanosoma* disappeared during eutrophication, but quickly re-established with the re-oligotrophication of the lake (Stich 2004). In shallow Lake Kraenepoel, Belgium, *Diaphanosoma* dominated the pre-alteration zooplankton community, regressed during eutrophication, and dominated again after the restoration of the lake (Louette et al. 2009). The authors argued that although the near absence of fish after restoration allowed the expansion of large *Daphnia* species, the reduction in nutrient level favoured *Diaphanosoma* over large *Daphnia,* which are known to grow best in productive systems (Jeppesen et al. 2003a; Declerck et al. 2007).

In Lake Vesijärvi, *Limnosida* and *Diaphanosoma* both increased in abundance during re-oligotrophication, which was seen in the sediment (V) and in the plankton data (II; Vakkilainen & Kairesalo 2005). In the RDA of surface sediment lakes, these species were at the opposite ends of the biplot, *Limnosida* associating more closely with large lakes. *Limnosida* feeds selectively on larger particles and thus hardly competes with microfilterers, such as *Diaphanosoma* and many daphnids (Jensen et al. 2001). Although *Limnosida* apparently tolerates moderate fish predation (Hessen et al. 1995), it is positively selected by fish (Alajärvi & Horppila 2004). Therefore, it probably benefited from fish reduction and re-oligotrophication, since it seems to prefer lakes with low calcium and phosphorus concentrations (Flößner 2000; Jensen et al. 2001). In the set of 31 lakes, however, *Limnosida* associated closely with high conductivity. Karjalainen et al. (1999) compared zooplankton communities along a trophic gradient in two bays in Lake Ladoga and found more *Limnosida* in the vicinity of the main loading point. The authors suggested, however, that water depth might have also affected the result.

The observed pattern after fish reduction in Lake Vesijärvi was very similar to Lake Gjersjøen, Norway, where the proportion of *Daphnia* remained low after fish reduction and *Limnosida* increased in abundance (Lyche et al. 1990). The abundance of *Daphnia* ephippia in Lake Vesijärvi was higher in the sediment varve of 1994, just after efficient fishing of the lake. The number of *Daphnia* claws did not increase, but uncertainties in the quantitative retention of small claws may obscure the result. *Daphnia* densities also increased in 1994 according to plankton data (Luokkanen 1995; Fig. 3 in V), but a sustained increase in *Daphnia* abundance was not observed, contrasting with the common expectation of biomanipulation (e.g. Hansson et al. 1998). Jeppesen et al. (2005) found that, along with the re-oligotrophication and decreasing fish stocks, the contribution of *Daphnia* to total zooplankton biomass increased in shallow lakes but not in deep lakes. The authors suspected that a stronger response in shallow lakes reflected an apparently higher predation risk in such lakes (Keller & Conlon 1994; Jeppesen et al. 1997; Jeppesen et al. 2003a). The result could also be related to the *Daphnia* species concerned, as the generally small *Daphnia* species inhabiting boreal lakes (Rahkola-Sorsa 2008) as well as the pelagic zone of Lake Vesijärvi (i.e. *D. cucullata, D. longiremis* and *D. cristata;* and *D. cristata* also in Lake Gjersjøen) tolerate relatively high fish densities (Mazumder 1994; Hessen et al. 1995). The remains of species belonging to the *Daphnia longispina* species complex cannot be identified at the species level (but see Korosi et al. 2011), and the relative changes of *Daphnia* species were not therefore revealed in the sediment records. This may partly explain the poor correlation between *Daphnia* and the trophic gradient also observed in the set of 31 lakes. According to Sammalkorpi (1995), *D. cristata* was the most common daphnid species until the 1960s, when *D. cucullata* appeared and already by the 1980s became the most important daphnid in the late summer zooplankton. *D. cucullata* tolerates large filamentous cyanobacteria, and is thus favoured in eutrophication (Hawkins & Lampert 1989; Gliwicz 1990b). According to zooplankton records from 1991 onwards, *D. cucullata* remained as the most important *Daphnia* species after fish manipulation, although its abundance as well as that of *D. longiremis* decreased slightly after the peak in 1994, and that of *D. cristata* increased (K. Vakkilainen, unpublished zooplankton data). The recent zooplankton samples have revealed further changes, as *Daphnia galeata* appeared in Lake Vesijärvi, although at a very low abundance (M. Ketola, unpublished zooplankton results from 2009 and 2011).

Overall, the pelagic species composition in southern Finland, inferred from lake sediments, was clearly related to the trophic gradient. Rather than the presence or absence of single indicator species, subtle changes in the relative species composition characterise the lake condititions. This result is in accordance with previous observations of cladoceran communities (Korhola & Rautio 2001). For example, Davison et al. (2010) investigated 39 shallow lakes in the U.K. and Denmark, and concluded that a species-driven, but community-based approach reflected differences in ecosystem function associated with nutrient enrichment. Hann et al. (1994) observed changes in the relative abundance of species rather than species replacements in response to experimental eutrophication in Lake 227 of the Experimental Lakes Area, Ontario. They also observed some time lag in the response of the community composition, despite strong experimental treatment. Resistance or temporal delays in the change in species composition have also been observed after fish introductions (Räsänen et al. 1992; Perga et al. 2010) and in response to re-oligotrophication (Straile & Geller 1998; Jeppesen et al. 2005; Manca et al. 2007). Although subtle, the initial response of the community composition in Lake Vesijärvi was rather rapid, probably owing to the drastic reduction in fish density. However several species did not respond. Further changes in pelagic species composition are possibly expected in time along with re-oligotrophication, as indicated by the appearance of *Daphnia galeata*, 15 years after fish manipulation.

If not an artefact of the sedimentation process, the total concentration of cladoceran remains indicated a peak in abundance in 1994, just after the fish manipulation. The grazing rate of the zooplankton community probably increased, as indicated by the decreased ratio of chl-*a* to total phosphorus (Fig. 6). In Lake Pyhäjärvi, Finland, Helminen and Sarvala (1997) observed strong top-down effects as a response to variable recruitment of the main planktivore, vendace (*Coregonus albula*), even though the zooplankton consisted of relatively small species (<1.2 mm). Therefore, grazer control of algae in mesoeutrophic systems does not necessarily demand large cladocerans (Helminen & Sarvala 1997), but their total biomass is decisive (Sarvala et al. 1998).

Littoral species and total diversity

The concentration of littoral remains in Lake Vesijärvi increased in the postmanipulation period (Table 2 in V), and most evidently increased the concentration of plant-associated species (Fig. 6 and Table 2 in V). A marginally insignificant increase (p = 0.059) was observed in the concentration of rock- or sand-associated species, while changes in the concentration of mud-dwelling species were very similar to those of planktonic species. After fish manipulation, submerged macrophytes expanded from depths of 2 m to as much as 4 m in Lake Vesijärvi (Venetvaara & Lammi 1995), increasing the potential area in the basin covered by vegetation from 18% to 33% (Vakkilainen 2005). The increase in the concentration of littoral, and especially plant-associated species, as well as a consequent decrease in the P/L ratio, probably resulted from the expansion of submerged macrophytes, providing more habitats for plant-associated species (cf. Thoms et al. 1999).

The inverse relation of the maximum depth distribution of submerged macrophytes to the total phosphorus concentration has been reported, for instance, in a Danish lake set (Søndergaard et al. 2005). As no quantitative information on macrophyte coverage was available for the set of 31 study lakes, the Secchi/mean depth was used as a surrogate for the potential of benthic production (cf. Bjerring et al. 2009). This variable correlated negatively with total phosphorus concentration (Table 2). The concentration of plant-associated species was positively related to the Secchi/mean depth ($r^2 = 0.336$; $p = 0.001$), while the P/L ratio$_{\log}$ showed a significant inverse relationship ($r^2 = 0.266$; $p = 0.003$), suggesting a dominance of planktonic species in lakes with low transparency in relation to mean depth. The abundances of rock- or mud-associated species were not related to the Secchi/mean depth ($p > 0.05$). The availability of rocky habitat in the lake set was probably connected to other factors. Rocky or sandy shores are characteristic of large Finnish lakes. In fact, the abundances of both rock- and mud-associated species were positively related to lake area$_{\log}$ (rock-associated species$_{\log}$ $r^2 = 0.331$; $p = 0.001$; mud-associated species$_{\log}$ $r^2 = 0.207$; $p = 0.010$). The results for the 31 lakes thus supported the view that the increased abundance of plant-associated species in Lake Vesijärvi was connected to the expansion of submerged macrophytes. Because young roach in the Enonselkä basin feed in the littoral zone (Horppila et al. 1996), littoral cladocerans could also have benefited from the reduced fish population. However, no increase in the ratio of large species to total littoral species to was observed after fish manipulation (see chapter 4.3).

Shannon's diversity index for the entire subfossil cladoceran community (pelagic and littoral) also increased after fish manipulation in Lake Vesijärvi (period IV; Fig. 6 and Table 2 in V). In the set of 31 lakes, Shannon's diversity index, as well as the total number of taxa, were negatively related to TP$_{\log}$ (diversity $r^2 = 0.135$; $p = 0.042$; taxa number $r^2 = 0.166$; $p = 0.023$). An inverse relationship between cladoceran diversity and nutrient status or primary production has been recorded elsewhere, especially for chydorids but also for planktonic cladocerans (Whiteside & Harmsworth 1967; Whiteside 1970; Amsinck et al. 2005; Declerck et al. 2007). The adverse effect of eutrophication on chydorid diversity seems to mainly operate through habitat availability, as species strictly associated with vegetation are lost together with submerged vegetation (Whiteside 1970; Hofmann 1987; Declerck et al. 2007). With planktonic species the possible mechanism is more controversial, but probably involves multiple factors, such as food quality, competitive displacement, predation effects, as well as a deterioration in abiotic conditions (Dodson et al. 2000; Declerck et al. 2007). Amsinck et al. (2005) observed a decrease in cladoceran species richness with increasing salinity, TP and TN, but no association with planktivorous fish density, macrophyte coverage or lake surface area in a set of 36 shallow brackish lakes in Denmark. The authors suspected that the decreasing diversity with increasing TP without the relevance of submerged macrophytes was indirect, because salinity and TP were correlated. In the set of 31 lakes of this study, the association of total diversity with the Secchi/mean depth was not significant ($p > 0.05$), possibly because of the inclusion of planktonic species. The diversity index was also unrelated to the lake area ($p > 0.05$), although the concentrations of rock- and mud-associated species increased as a function of lake area. A positive association between diversity and lake area has been found elsewhere (Dodson et al. 2000), but not always (Whiteside & Harmsworth 1967; Hessen et al. 2006). Hessen et al. (2006) studied Norwegian lakes, focusing on the pelagic zooplankton. Most of their study lakes were oligotrophic, and the diversity of pelagic cladocerans increased linearly with lake productivity. Some other studies with longer nutrient gradients have detected a unimodal relationsphip between cladoceran species richness and lake production (Dodson et al. 2000; Jeppesen et al. 2000a; but see Declerck et al. 2007). This initial increase in diversity was not seen in the set of 31 lakes of this study.

Main structuring forces

Both bottom-up and top-down forces affect zooplankton biomass and size structure simultaneously, in addition to physical factors, and it is often difficult to interpret the relative strengths of each factor across lakes (Carpenter et al. 1985; McQueen et al. 1986; Power 1992; Finlay et al. 2007). The total phosphorus concentration and the biomass of planktivorous fish were highly correlated in the data set of 31 lakes, and they both decreased in Lake Vesijärvi during the study period. Many of the surface sediment data sets for inferring TP do not include fish data (e.g. Bos & Cumming 2003). Lotter et al. (1998) found a stronger association with epilimnetic TP in benthic cladoceran assemblages than in planktonic cladocerans in small alpine lakes, Switzerland, but did not discuss possible predators. Brodersen et al. (1998) included only chydorids in the TP model for Danish lakes, assuming indirect effects through changing microhabitats, substrates, food and oxygen regimes, and did not include fish data. Instead, Jeppesen et al. (1996) found a significant relationship between selected planktonic taxa and planktivorous fish abundance in Danish lakes, and inclusion of TP improved the model between zooplankton and fish. Amsinck et al. (2005) developed a more reliable inference model for planktivorous fish CPUE in brackish lakes by using all taxa instead of solely pelagic taxa. Inference models for TP and salinity were also significant, but TP and salinity were highly correlated, hampering the interpretations. Both the model of Jeppesen et al. (1996) and that of Amsinck et al. (2005) for fish CPUE were less precise than those of Brodersen et al. (1998) and Bos & Cumming (2003) for TP. More uncertainties are involved in the estimation of fish abundance than of TP in lakes, which may partly explain the higher root-mean-squared error of prediction (RMSEP) values in fish models (Jeppesen et al. 1996; Amsinck et al. 2005). When fish are quantified, however, they appear to have a pronounced influence on zooplankton. Brugam and Speziale (1983), focusing on planktonic remains and carrying out size measurements, concluded that the subfossil zooplankton was a more sensitive indicator of the history of predation than of the lake trophic status in Lake Harriet, Minnesota.

To better extract the main structuring forces affecting cladoceran communities in the set of 31 lakes of this study, a series of RDA ordinations was run, taking only one environmental variable at a time and the remainder as covariables (partial RDA). This prodecure allows estimation of the contribution of each variable to the explanatory power (Borcard et al. 1992; ter Braak 1995). The unique contribution of the environmental variables was much lower than their explanatory power as sole variables, without other variables as covariables (Table 3). In general, over 60% of the variance explained by each variable originated from the interaction with the other variables. While LOI% and conductivity explained most of the variance as sole variables, the biomass of

Table 3. Results of the constrained (variance explained) and partial (unique contribution) RDA for 14 environmental variables of 31 study lakes. Interaction (%) indicates the covariance of each variable with other environmental variables. The Monte Carlo permutation procedure was used to investigate the statistical significance of the first axis in the constrained ordination of sole variable.

Parameter	**Variance explained (%)**	**Unique contribution (%)**	**Interaction (%)**
LOI%	**23.8	3.0	65.2
Surface area	**17.3	3.7	64.5
Mean depth	7.1	2.9	65.3
Maximum depth	*7.7	2.7	65.5
pH	**16.9	0.7	67.5
Conductivity	**23.4	1.0	67.2
Colour	4.3	1.6	66.6
Total N	*9.0	2.2	66.0
Total P	**13.0	3.9	64.3
Secchi depth	10.8	2.1	66.1
Fish size,	*11.1	1.7	66.5
Planktivorous fish B	**17.1	6.8	61.4
Benthivorous fish B	4.9	1.0	67.1
Piscivorous fish B	3.9	1.8	66.4

Significance levels: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***

planktivorous fish had the highest unique contribution (6.8%) in explaining variance in subfossil assemblages. The total phosphorus concentration (3.9%) and surface area (3.7%) followed next.

Environmental data were grouped into three components: morphometry (max. depth, mean depth, surface area, LOI%), chemistry (total N, total P, pH, conductivity, colour, Secchi depth) and fish component (fish size and biomasses of plankti-, benthi- and piscivorous fish). Variance partitioning was used to detect how the variation in the species response was partitioned according to these three components (Borcard et al. 1992). Morphometry had the highest contribution (15.2%) in structuring the species assemblages in this data set (Fig. 8). The chemical component (12.5%) was slightly more important than fish (10.7%). Covariation between the chemical component and fish (7.1%), between the chemical and morphological components (6.1%), and among all three components (14.6%) were appreciably high.

The great importance of lake morphometry in shaping community structure has been observed before with cladocerans (Keller & Conlon 1994; Korhola et al. 2000; Bos & Cumming 2003; Amsinck et al. 2006; Sweetman & Smol 2006; Kattel et al. 2008), as well as with other animal communities, including benthic macroinvertebrates (Jyväsjärvi et al. 2009) and fish (Olin et al. 2002; Mehner et al. 2005). A plausible explanation, especially in clear-water lakes, is the greater proportion of littoral habitat in shallow lakes than in deep lakes, affecting the relative importance of pelagic and littoral species (Alhonen 1970; Korhola et al. 2000; Amsinck et al. 2006). Olin et al. (2002) studied 36 lakes in southern Finland, many of which were the same as in this study. At a given nutrient level they observed a higher cyprinid biomass in shallow than in deep lakes, and in large rather than in small lakes. Therefore, lake size affected the fish community changes in relation to TP, which may have implications for zooplankton prey (cf. Keller & Conlon 1994; Jeppesen et al. 1997; Jeppesen et al. 2003a). Lake morphometry affects the strength of benthic-pelagic links, and thus the overall importance of benthic processes in lakes (Vadeboncoeur et al. 2002). For instance, the biomass of benthic invertebrates, representing alternative prey, is higher in shallow lakes, making benthi-planktivorous fish less dependent on zooplankton than in deep lakes (Jeppesen et al. 1997). In deep lakes the hypolimnion provides an additional habitat for zooplankton, allowing the coexistence of distinct species communities, and serving as potential vertical refugia from fish predation (Kitchell & Kitchell 1980; Lampert 1989; Keller & Conlon 1994). Therefore, lake size and depth are critical for the habitat structure of living cladocerans, but they also influence the taphonomic zones, i.e. where and how the remains are deposited.

In this study, littoral species were only included as habitat groups, giving more weight to pelagic species. Although morphological variables were the main structuring force as a whole, planktivorous fish biomass was the most important sole variable structuring cladoceran assemblages, followed by TP. It is evident, however, that multicollinearity of environmental variables, as well as differing morphometries and sedimentary conditions among the lakes obscured the detection of individual species responses to lake trophic status or to fish predation. Therefore, when discriminating anthropogenic disturbance from natural covariates, the effect of morphometry has to be taken into account. In a site-specific approach, however, the variance attributable to morphometry is essentially removed, if water level has remained the same in the time scale of anthropogenic influence. Hence, when studying recent sediments of a single lake, zooplankton remains should be even stronger predictors of lake ecological quality than suggested by the results from 31 lakes of differing morphometry.

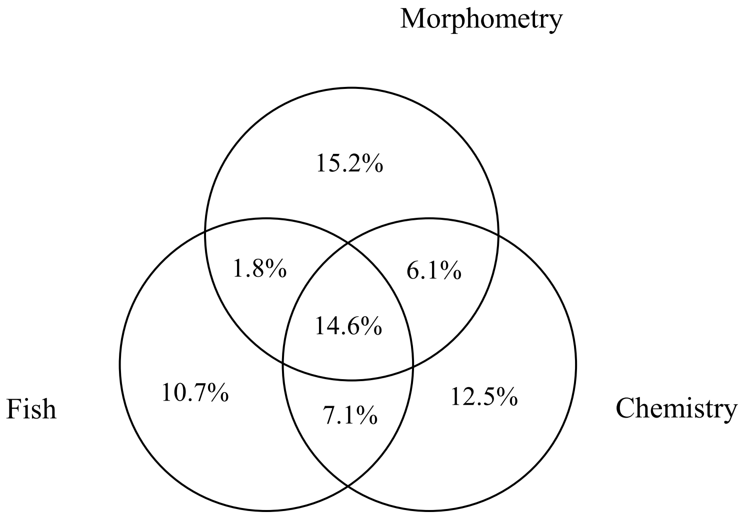

Figure 8. Variance in species response partitioned according to environmental variables, which were divided into three components: morphometry (max. depth, mean depth, surface area, LOI%), chemistry (total N, total P, pH, conductivity, colour, Secchi depth) and fish (fish size and biomasses of planktivorous, benthivorous and piscivorous fish).

4.3 Specific indices of predation

Size of cladocerans

Size as an indicator of fish predation can be taken as the size structure of the zooplankton community or as the body size of individual species. Moss et al. (2003) proposed a ratio of the numbers of large species (>0.5 mm) to the total numbers of Cladocera as an indicator of community changes along a trophic and ecological quality gradient. Sarvala et al. (1998) used this size limit and found a lower proportion of large cladocerans in years with strong stocks of planktivorous fish, when studying long-term data from Lake Pyhäjärvi, Finland. In a set of 25 lakes with zooplankton data available, the ratio of large species to the total density of Cladocera correlated positively with Secchi depth ($r_s = 0.492$, $p < 0.05$), implying that large species were found together with high levels of transparency (I). Furthermore, a negative correlation between chlorophyll-a and the ratio between zooplankton and phytoplankton biomass ($r_s = -0.622$, $p < 0.01$) was indicative of the potential ability for zooplankton to control phytoplankton biomass in lakes with low levels of chlorophyll-a (I). In Lake Vesijärvi, the ratio chl-a:TP decreased (Fig. 6) in the period of lowest fish density, indicating more efficient grazing (Mazumder 1994; Sarvala et al. 1998). The subfossil ratio of large species to the total species pool of cladocera, however, did not indicate any changes between the fish periods (Kruskal-Wallis test $p > 0.05$) for solely pelagic species, littoral species, or all species. The result was in accordance with the plankton results of Vakkilainen (2005), who observed no changes in the density-weighted mean body length of cladocerans in the 1990s after fish manipulation.

In the set of 31 lakes the size ratio behaved differently depending on whether pelagic, littoral or all cladocerans were considered. There was a significant inverse relationship between the ratio based on pelagic species (large:total pelagic$_{sqrt}$) and planktivorous BCPUE$_{log}$ ($r^2 = 0.24$; $p = 0.005$) and TP$_{log}$ ($r^2 = 0.33$; $p = 0.001$). In contrast to pelagic species, a ratio based on littoral species (large:total littoral) was weakly, but positively, related to planktivorous BCPUE$_{log}$ ($r^2 = 0.13$; $p = 0.043$), and not related to TP$_{log}$ ($p > 0.05$). The ratio based on all species (large:total all$_{sqrt}$) was not related to planktivorous BCPUE$_{log}$ ($p > 0.05$), but decreased with TP$_{log}$ ($r^2 = 0.43$; $p < 0.001$). Thus, in this Finnish lake set the ratio of large to total cladocerans most reliably indicated lake trophic structure if based on pelagic species. In the littoral zone, other structuring forces than size-selective fish predation may be more important. However, the 0+ age class of fish can be important predators in littoral zones (Whiteside 1988), although the early stages are gape-limited and therefore select smaller prey. The food consumption of young fish is not properly reflected in the fish biomass estimate based on gill netting. Nilssen and Sandøy (1990) measured the size of large littoral Chydoridae in 18 Norwegian lakes, but did not find a clear relationship with fish predation. The ratio based on both pelagic and littoral species responded negatively to the total phosphorus concentration, however, possibly because the relative abundance of planktonic species (P/L ratio$_{log}$) increased with TP$_{log}$ ($r^2 = 0.18$; $p = 0.017$).

Although the ratio of large to total pelagic cladocerans appears a useful indicator of community structure on the basis of the set of 31 lakes in this study, in Lake Vesijärvi it was not sensitive enough to detect the changes over a relatively short period. Manca et al. (2007) and Bjerring et al. (2009) divided subfossil species into three size groups, which might comprise a more sensitive indicator. The average body size of individual taxa, however, responded rapidly and clearly to changing fish predation in Lake Vesijärvi (III, V). A significant increase was observed in the average size of *Daphnia* ephippia, *Bosmina (E.) crassicornis* ephippia and carapaces, and *Bosmina longirostris* carapaces after the reduction in the fish population (V). The response of the mean size of the cladoceran population to a high level of fish predation may be direct, as visually hunting fish remove large prey individuals. This may lead to genetical adaptation of the population (e.g. Pace et al. 1984), if the remaining individuals belong to clones that are able to start reproduction at a smaller size. Size at first reproduction is an important life history trait of cladocerans in size selective predation (Lynch 1980). In addition to genetic adaptation, phenotypic plasticity, also observed among cladocerans, offers an effective and rapid mechanism of adaptation to changes in fish predation (Černý & Bytel 1991; Macháček 1991; Stibor 1992; Lambert 1993). Cladocerans are able to change their life history traits even as a response to kairomones, chemical cues of predators (Macháček 1991; Stibor 1992). The mean body size is a powerful indicator of fish predation, but cladoceran size is additionally related to some other factors (cf. Korosi et al. 2010). For instance, cold water may decrease the growth rate and moulting frequency (Manca & Comoli 2004), while a high temperature can lead to decreased feeding efficiency and a smaller body size at maturity (Korosi et al. 2010). A large body size enhances resistance to starvation at low food concentrations (Threlkeld 1976), but a low food concentration also reduces the growth rate (Wegleńska 1971). Further, a reduction in body size may be advantageous in cyanobacterial blooms (Lampert 1982, Hawkins & Lampert 1989). The disappearance of cyanobacteria and the reduction of planktivorous fish should both have selected for a larger body size in Lake Vesijärvi.

In sediment studies, size measurements of *Daphnia* have been carried out for ephippia (Verschuren & Marnell 1997; Jeppesen et al. 2002), postabdominal claws (Kitchell & Kitchell 1980; Perga et al. 2010) and mandibles (Kerfoot 1974). Manca and Comoli (1996) demonstrated that claws provide a more reliable estimate of body length than mandibles, but relatively large changes in body length were needed (>200 µm) to statistically differentiate changes. In this study, the retention as well as the preservation of the claws of small *Daphnia* species was uncertain and only ephippia were measured. The size of *Daphnia* ephippia is in direct relation to the size of the egg-bearing female (Verschuren & Marnell 1997; Jeppesen et al. 2002). As cladocerans only produce ephippia during certain time periods, the size of ephippia reflects the size of mature females in the population only at the time of ephippia production, not necessarily during the whole season. The ephippial females are, however, even more susceptible to fish predation than nonephippial females due to their greater visibility (Mellors 1975). Jeppesen et al. (2002) found a significant negative relationship between fish CPUE and the mean size of *Daphnia* ephippia in the surface sediment of 52 mainly shallow lakes. In that lake set, ephippia size was also related to the mean summer weight of *Daphnia* in the lake pelagial. The authors proposed the mean size of *Daphnia* ephippia as a useful method to quantify planktivorous fish abundance. The results of the present study supported this method, although with some constraints. *Daphnia* ephippia were sometimes worn, preventing accurate measurement (varve 2001; III; V). They can also be relatively infrequent, so that large amounts of sediment need to be screened to attain a reliable estimate of the mean size (personal observation).

Care should also be taken, as genus-level identification of *Daphnia* remains may mask species replacements attributable to other factors than predation, e.g. pH (Korosi et al. 2010).

Bosmina carapaces have also been measured to reconstruct fish predation (Salo et al. 1989; Hann et al. 1994; Sweetman & Finney 2003). In Lake Vesijärvi, reduced fish predation was seen in the increased size of *B. longirostris* carapaces, and *B. (E.) crassicornis* carapaces and ephippia (V). *B. (E.) longispina* was too scarce for reliable measurements. The result was well in accordance with the knowledge that *Bosmina*, and especially the epilimentic *B. (E.) crassicornis*, encountered heavy predation by roach in Lake Vesijärvi (Horppila et al. 2000), which was one of the main targets of efficient fishing. Nevertheless, even the mean size of the smallest *Bosmina* species, hypolimnetic *B. longirostris*, increased. Changes in the mean size and life-history traits of *B. longirostris* have previously been observed in fish enclosures (Ślusarczyk 1997), as well as in lake littoral zones under size-selective fish predation (Kerfoot 1981).

Bosmina carapaces were measured from the set of 31 lakes to further test the response of *Bosmina* size to fish predation. No significant relationship to fish was found at the species level, but the mean size of *Bosmina* spp. (all species combined) was negatively related to both $\mathrm{BCPUE}_{\log}$ ($r^2 = 0.17$; $p = 0.022$) and $\mathrm{TP}_{\log}$ ($r^2 = 0.39$; $p < 0.001$). At the species level the mean size of *B. (E.) cf. coregoni* decreased with $\mathrm{TP}_{\log}$ ($r^2 = 0.75$; $p < 0.001$, $n = 15$). However, some caution is necessary when considering the attained significance levels for *B. (E.) cf. coregoni*, as the size of this species was not normally distributed, even after transformation (Shapiro-Wilk test of normality, $p < 0.05$). Not all *Bosmina* species were found in sufficient numbers from every lake, and thus a lower number of samples may partly explain the few significant relationships at the species level. While *B. longirostris* was most abundant in eutrophic and brownwater lakes, *B. (E.) longispina* was abundant in clear-water lakes with a low fish density and nutrient level (Fig. 7c). As *B. longirostris* is generally smaller than *B. (E.) longispina*, the mean size of *Bosmina* spp. also reflects the changes in species composition along the trophic gradient. According to the hypothesis of Faustová *et al.* (2010; 2011), stating that eutrophication and predatory interactions are driving forces for a relatively recent speciation of *Eubosmina* in Europe, *B. (E.) cf. coregoni* (incl. *coregoni, crassicornis, longicornis*), in particular, should be highly adaptable to changes in lake trophy and fish density. The strong relationship between the mean size of *B. (E.) cf. coregoni* and total phosphorus in the set of 31 lakes, as well as the observed changes in Lake Vesijärvi supported this hypothesis. In the recent sediment of Lake Pyhäjärvi, Salo et al. (1989) found a decrease in the mean size of *B. (E.) coregoni*, related to the introduction of whitefish (*Coregonius lavaretus* s.l.), for which *B. (E.) coregoni* was the most important prey species. Although the mean size of *B. (E.) coregoni* responded, the relative species composition remained stable (Räsänen et al. 1992).

As stated before, the abundance of planktivorous fish was positively correlated with the total phosphorus concentration in this data set (Table 2). In reality, the correlation may be even stronger, because there is likely to be considerable variation in the biomass estimate of fish (BCPUE), even though standard gillnetting was used. Although fishing effort was adjusted in relation to lake area, it varied between the lakes from 0.03 to 2.22 nets ha^{-1}. Any passive method is selective and dependent on fish movements (Kurkilahti 1999). Therefore, there may be large spatial and interannual variation in the catches (Jeppesen et al. 1996). Although 0+ fish are important planktivores (Whiteside 1988; Kurmayer & Wanzenböck 1996), their inclusion in fish catches is especially variable, as well as their survival in the first few months.

Other indices

The size and shape of the antennula and mucro of *Bosmina longirostris* are indicative of invertebrate predation, especially by copepods (O'Brien & Schmidt 1979; Kerfoot 1981; 1987; Sanford 1993; Sweetman & Finney 2003: Alexander & Hotchkiss 2010). The long-featured form is better protected against cyclopoids than the short-featured form, *Bosmina longirostris* var. *cornuta* (Jurine), because copepods must expose the soft, ventral body surface of *Bosmina* for ingestion (Kerfoot 1978; Sakamoto et al. 2007; Sakamoto & Hanazato 2008). Long mucros increase the handling time, allowing an opportunity to escape. Straight antennules also aid in tucking the swimming appendages to sink away from the predator (Kerfoot 1978). It has been hypothesized that the *cornuta* form can only exist when fish control the abundance of invertebrate predators. Thus, the relative percentage of the *cornuta* form in *Bosmina longirostris* morphotypes could serve as an indicator of fish predation (Sanford 1993; Leavitt et al. 1993; 1994). In Lake Vesijärvi, no correlation was found between *cornuta*% and fish abundance (V). The reduction of the fish population in the lake may not have led to changes in copepod predators, or the signal may have been mixed with fluxes of possibly abundant littoral populations of the *cornuta* form (cf. Sanford 1993). According to the subfossil record, no significant changes in the abundance of other invertebrate predators, *Leptodora* and *Bythotrephes*, occurred after fish manipulation (V). In the set of 31 lakes, however, $cornuta\%_{sqrt}$ increased with the planktivorous $\mathrm{BCPUE}_{\log}$ ($r^2 = 0.386$; $p < 0.001$), suggesting the applicability of this index at least in some cases in Finland.

The ratio *Daphnia/(Daphnia+ Bosmina)* has previously been used as a 'fish index' (Kitchell & Kitchell 1980; Leavitt et al. 1989; 1994; Hann et al. 1994; Jeppesen et al. 2003b; Manca et al. 2007), but it may only be applicable in lakes where large *Daphnia* species (>1 mm) exist (Hann et al. 1994). In Lake Vesijärvi the coexistence of small *Daphnia* species with fish, as well as the consumption of bosminids by roach, both complicated the use of this index, and based on parthenogenetic remains, no trend was found. In the set of 31 lakes the ratio $Daphnia/(Daphnia+Bosmina)_{sqrt}$ decreased with $\mathrm{TP}_{\log}$ ($r^2 = 0.139$; $p < 0.039$) and planktivorous $\mathrm{BCPUE}_{\log}$, but the relationship with fish was marginally nonsignificant ($r^2 = 0.112$; $p < 0.065$). The ratio based on parthenogenetic remains probably suffers from the uncertain retention of daphniid claws. Manca et al. (2007) found a close agreement between the indices based on sedimentary remains and contemporary data, but with different scales, implying the underprepresentation of *Daphnia* in the sediment. Ephippia, which are more reliably retained, have also been used in the ratio (Jeppesen et al. 2003b; 2011). Problems arise if the intensity of ephippial production varies between years (Frey 1982; Jankowski & Straile 2003; Keller & Spaak 2004; Tsugeki et al. 2008; V). When based on ephippia and solely on the epilimnetic *B. (E.) crassicornis*, the index increased from 1992 onwards, when a major drop in the fish density was observed in Lake Vesijärvi (V). However, the ephippium% [ephippia / (parthenogenetic remains + ephippia) × 100%] of *B.* (*E.) crassicornis* decreased towards the 2000s (V), affecting the ratio.

Ephippial production is a normal strategy for the overwintering of several cladoceran species. Longer growing seasons with increasing temperatures can lead to prolonged periods of parthenogenetic reproduction, and consequently to lower percentages of ephippia in relation to parthenogenetic remains (cf. Jeppesen *et al*. 2003b; Sarmaja-Korjonen 2003; 2004). Tsugeki et al. (2008) observed a clear decrease in the flux of ephippia to the sediment in Lake Biwa since the 1980s, even though the *Daphnia galeata* population remained abundant in the plankton community. The authors connected the observed discrepancy to enhanced conditions for overwintering as parthenogenetic females, resulting from winter warming. In addition to water temperature and day length, gamogenesis may be induced by the predation risk, crowding, food depletion and oxygen availability (Carvalho & Huges 1983; Ślusarczyk 1995; 2001; Pijanowska & Stolpe 1996; Nevalainen et al. 2011). Thus, trophic changes may also have implications for the ephippium production of cladocerans (cf. Jankowski & Straile 2003; Jeppesen et al. 2003b; Sarmaja-Korjonen 2003; 2004).

In Lake Vesijärvi the ephippium% of *B. (E.) crassicornis* and *B. longirostris* showed different patterns seasonally (II), and annually after fish manipulation (V). The pressure initiating ephippial production probably differs between these species because of their different vertical habitat preferences. The epilimnetic *B. (E.) crassicornis* had a lower ephippium% (1−6%, mean 3%) than the hypolimnetic *B. longirostris* (combined with *B. (E.) longispina;* 3−16%, mean 6%). The difference was minimal before the fish manipulation, but expanded in the postmanipulation periods (V; III). As *B. (E.) crassicornis* produced most of its ephippia in autumn (II), the increased late summer (August, September) epilimnetic water temperature in the post-manipulation period possibly contributed to the observed decrease in the ephippium% at the end of study period (V). In contrast, the ephippium% of *B. longirostris* increased and varied considerably after the fish manipulation. In the hypolimnion, *B. longirostris* and *B. longispina* may encounter different environmental constrains compared to epilimnetic species, such as insufficient oxygen availability. In 2002, *B. longirostris* already produced ephippia in June, after reaching a density of >300 ind. L^{-1} (II). Such a short but intensive period of parthenogenetic population growth, followed by a population collapse, could lead to a high ephippium% in the sedimentary remains (V). Thus, the changes in the ephippium% after fish manipulation were evident in Lake Vesijärvi, but the ultimate reasons were difficult to interpret. In the set of 31 lakes, not enough ephippia were retained to draw any conclusions about the generality of the observed changes.

5. CONCLUSIONS

The correct interpretation of palaeolimnological records demands not only understanding of the ecological significance of observed changes in the sediment, but also understanding of the taphonomic processes that affect the signal. The comparison of cladoceran remains in the annually laminated sediment of Lake Vesijärvi with contemporary zooplankton data revealed a good representation of ‘well-preserved species’ in the sediment, i.e. all three *Bosmina* species, *Chydorus sphaericus, Limnosida frontosa* and *Leptodora kindtii*. Net accumulation values similar to or exceeding the expected values indicated a minor loss of remains of these species. The difference in the accumulation to production ratios between epi- and hypolimnetic species was in accordance with the relative volumes of epi- and hypolimnion (2:1) in the lake, illustrating the importance of horizontal fluxes in sediment accumulation. The great excess of *Limnosida* and *Leptodora* in the sediment compared to the zooplankton records further supported this interpretation, as these species were probably more abundant in the shallower pelagial than at the zooplankton sampling point. The result was also in accordance with earlier studies on sedimentation dynamics in Lake Vesijärvi, which indicated a high resuspension rate in the lake, increasing the settling flux in the deepwater area (Liukkonen et al. 1993; Koski-Vähälä et al. 2000). The few other studies directly comparing accumulation rates with production have recorded minor (Hall & Yan 1997, *Bythotrephes*), or excessive (Kerfoot 1995, *Bosmina*) dissolution of remains. The results from Lake Vesijärvi suggested minor dissolution of well-preserved species, but sediment focusing towards the deepwater area, i.e. horizontal fluxes, may effectively counteract degradation losses.

In contrast to the well-preserved species, the accumulation of *Daphnia, Ceriodaphnia* and *Diaphanosoma brachyurum* remains was only a fraction of the expected values. Much of this poor representation was, however, an effect of sediment processing with a 50-µm mesh. The result stresses the importance of using the same method when processing and counting samples to be compared, including the application of models derived from surface sediments to the core samples. Visible signs of dissolution, variable representation of various *Daphnia* remains in the surface sediments of 31 lakes, as well as the higher concentrations of remains of *Daphnia, Ceriodaphnia, Diaphanosoma* and *Holopedium gibberum* in organic sediments, suggested selective, lake-specific preservation of these remains. This interpretation is further supported by the total disappearance of these remains in some lakes (e.g. Rautio et al. 2000, *Holopedium*; Davidson et al. 2007, *Diaphanosoma*). Factors affecting the degradation of cladoceran remains demand further investigation, but preservation is apparently enhanced in organic sediments. Reliable estimates of the degradation rates of different species (including littoral species) would require experimental studies, however, to eliminate between-lake differences in the transportation of remains.

The species abundances expressed as accumulation or as concentration units clearly represented different aspects of sedimentation in Lake Vesijärvi. Assuming no changes in sediment redistribution along the years, the accumulation rate showed a decrease in zooplankton production along with lake re-oligotrophication. Concentration units, in turn, reflected changes in the lake trophic structure, demonstrating the higher importance of zooplankton after the biomanipulation. However, annual variation in the accumulation to production ratios, as well as the similarity in the accumulation rate of remains for several species, may imply that sediment focusing efficiency varied between years. Given the high resuspension rate in Lake Vesijärvi, variations are likely, despite the annual lamination. The concentration peak of several cladocerans after manipulation was not similarly recorded in the plankton samples. Whether this was a signal of the increasing importance of zooplankton in the pelagic ecosystem, or just an anomaly of sedimentation dynamics, remains unresolved. However, the findings strongly encourage the assessment of results in several units (concentration, accumulation and percentages) before drawing final conclusions about the historical changes in cladoceran communities.

Although taphonomic factors introduced unexplained variation, the pelagic species composition in southern Finland, inferred from surface sediments of 31 lakes, was clearly related to the trophic gradient. In Lake Vesijärvi, sediment analysis revealed a similar direction of change in pelagic cladoceran community composition to that in the zooplankton samples. Rather than the presence or absent of single indicator species, subtle changes in relative species composition characterised the lake conditions. This finding is in accordance with previous observations on cladoceran communities (Korhola & Rautio 2001). In Lake Vesijärvi, *Limnosida* and *Diaphanosoma* clearly increased in abundance along with the re-oligotrophication of the lake, while *Ceriodaphnia* and rotifers decreased in abundance. Overall, however, the changes in the community composition in Lake Vesijärvi were rather slight, and several species did not show any response despite the drastic reduction in fish abundance. Resistance or temporal delays in the change in zooplankton species composition in response to re-oligotrophication have been observed elsewhere (Straile & Geller 1998; Jeppesen et al. 2005; Manca et al. 2007), and more changes may appear over time.

In contrast to relative abundances, the size measurements of *Daphnia* ephippia and *Bosmina (E.) crassicornis* ephippia and carapaces responded rapidly and clearly to fish reduction, which was in close accordance with the food preference of smelt and roach, the main targets of effective fishing. The mean size of *Bosmina (E.) cf. coregoni* was also connected to the trophic gradient in the set of 31 lakes, suggesting adaptation of this species group to the changing predation regime. The density-weighted mean size of *Bosmina* spp. was additionally related to the trophic gradient, which was probably connected to the change from *B. (E.) longispina* to smaller *B. longirostris*. The lack of species-level identification of *Daphnia* remains may partly explain the observed poor association between *Daphnia* abundance and the trophic gradient among 31 lakes, as well as in Lake Vesijärvi sediment. In addition, the commonly used fish index *Daphnia/(Daphnia+Bosmina)* may not perform well in boreal lakes having small *Daphnia* species resistant to fish predation, further complicated by the variable preservation and retention of *Daphnia* remains.

The focus of this thesis research was on the trophic structure in the lake pelagial zone. The species rich assemblages in the littoral zone are, however, valuable in palaeolimnogical research. When grouped according to their preferred habitat type, these species remains proved to be useful indicators of vegetation change in Lake Vesijärvi. The results from the set of 31 lakes supported this conclusion, as the concentration of plant-associated species, as well as the P/L ratio, was related to the Secchi/mean depth, which was used as a surrogate for potential aquatic vegetation. An increase in total diversity with decreasing nutrient status was also found in both Lake Vesijärvi and in the set of 31 lakes. Diversity was probably linked to increased habitat availability for plant-associated species, but also to factors in the lake pelagic zone.

The sediment organic content and conductivity explained most of the variance in species composition as sole variables, but were correlated with several other environmental variables. High level of collinearity among environmental variables complicates cladoceran-based reconstructions of single environmental variables. The biomass of planktivorous fish had the highest unique contribution (6.8%) in explaining the variance in subfossil assemblages, followed by the total phosphorus concentration (3.9%) and surface area (3.7%). As a whole, lake morphometry together with sediment organic content explained the highest percentage of variance in the species data, stressing the importance of natural covariates. Therefore, the effect of lake morphometry and taphonomic conditions has to be taken into account when setting reference conditions or assessing anthropogenic disturbances over a set of lakes. In a site-specific approach, however, among-lake variance attributable to morphometry and taphonomy is reduced. Hence, when studying the recent sediments of an individual lake with a stable water level and sedimentation dynamics, zooplankton remains should provide even more powerful signals of change than those observed on the basis of surface sediment data sets.

At present, zooplankton are not included in the biological quality elements of the WFD, despite their central role in lake ecosystems and sensitivity to various anthropogenic stresses. Recently, Jeppesen et al. (2011) urged the inclusion of zooplankton, both contemporary and sufossil, in the WFD, and advocated further research to develop zooplankton-based metrics at the regional level throughout Europe. This thesis work tested several indicies based on sedimentary zooplankton remains, and many, although not all without some constraints, proved to be valuable indicators of lake ecological quality in southern Finland.

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