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Zooplankton as the indicator  
of ecological quality and  
fish predation in lake ecosystems



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## LIST OF ORIGINAL PUBLICATIONS

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

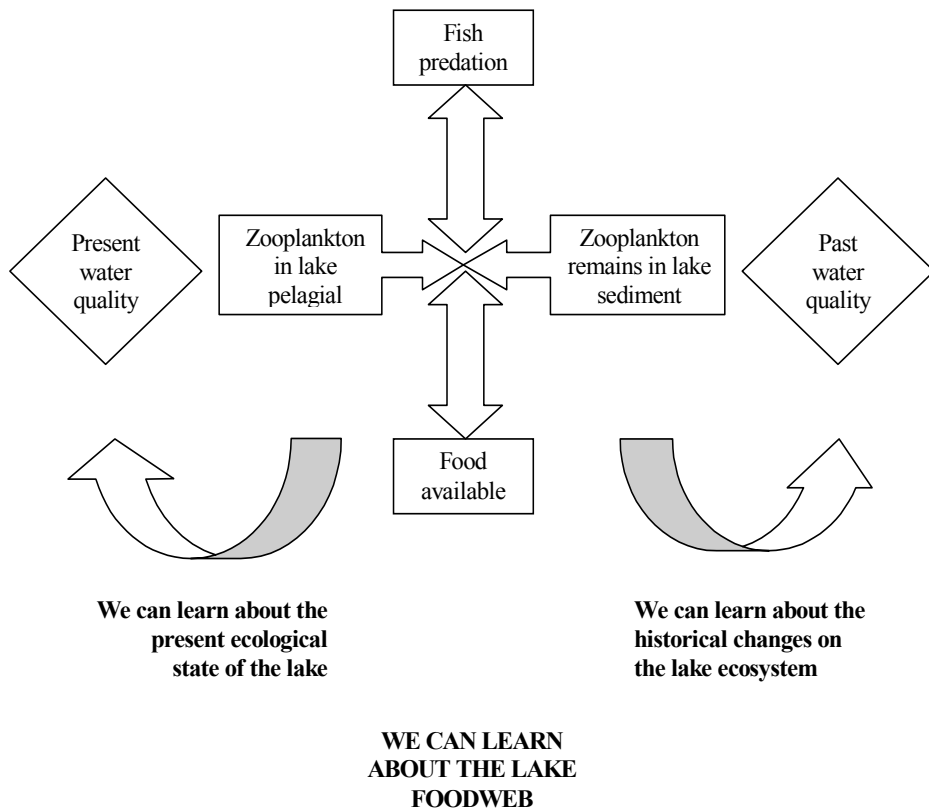
- I** de Eyto, E., Irvine, K., Garcia-Criado, F., Gyllstrom ,M., Jeppensen, E., Kornijow, R., Miracle, MR., Nykanen, M., Bareiss, C., Cerbin, S., Salujoe, J., Franken, R., Stephens, D. & Moss, B. 2003. The distribution of chydorids (Branchiopoda, Anomopoda) in European shallow lakes and its application to ecological quality monitoring. *Archiv für Hydrobiologie*, 156(2), 181–202.
- II** Nõges, P., Tuvikene, L., Feldmann, T., Tõnno, I., Künnap, H., Luup, H., Salujõe, J. & Nõges, T. 2003. The role of charophytes in increasing water transparency: a case study of two shallow lakes in Estonia. *Hydrobiologia*, 506(1–3), 567–573.
- III** Salujõe, J., Gottlob, H., Agasild, H., Haberman, J., Krause, T. & Zingel, P. 2008. Feeding of 0+ smelt *Osmerus eperlanus* in Lake Peipsi. *Estonian Journal of Ecology*, 57, 58–69.
- IV** Salujõe, J., Zingel, P. & Paaver, T. 2009. The cascading effects of predation by planktivorous juvenile fish on the microbial loop. (submitted to *Limnologia*).
- V** Alliksaar, T., Heinsalu, A., Saarse, L., Salujõe, J. & Veski, S. 2005. A 700-year decadal scale record of lake response to catchment land use from annually laminated lake sediments in southern Estonia. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 29(1), 457–460.

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	I	II	III	IV	V
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Study design			*	*	
Data collection	*	*	*	*	
Data analysis	*	*	*	*	*
Manuscript preparation	*	*	*	*	*

# I. INTRODUCTION

Zooplankton is a crucial link in lake food chains. The capacity of zooplankter to utilize primary producers and their suitability as food for fish determines the effectiveness of the lake food web. The more of the organic matter assimilated by algae that reaches the fish, the more efficient the food chain becomes. The remains of uneaten zooplankters accumulate in the lake sediment and can be back-tracked in sediment cores. Zooplankton communities are very dynamic and can respond to changes in the environment. So a lake's zooplankton provides us with information about both its present and past states (Fig. 1).

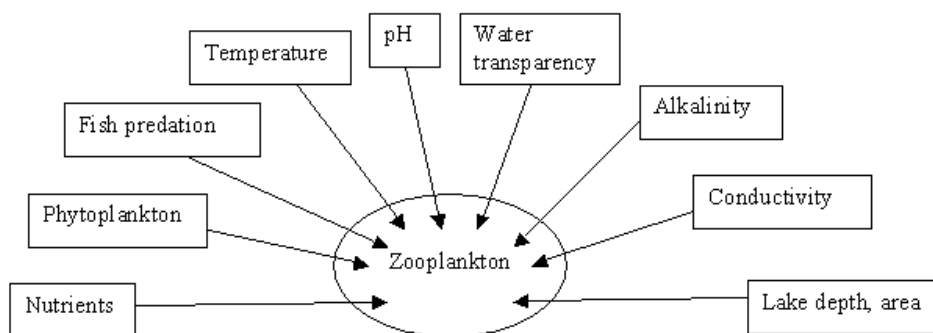


**Fig. 1.** Zooplankton is a suitable indicator of food web functioning and the ecological state of a lake.

## 2. REVIEW OF THE LITERATURE

### 2.1. Zooplankton is a complex indicator of lake water quality

Zooplankters respond quickly to environmental changes and may be effective indicators of subtle alterations in a lake. The most important question that could be addressed using zooplankton as an indicator of lake water quality is: which factors are most important in determining the distribution of zooplankton assemblages (Fig. 2)? Since most zooplankton species are found in a wide variety of lake types, the indicator value of individual species is somewhat limited to extreme oligotrophic or eutrophic conditions. In some instances, certain zooplankton species, especially rotifers, have apparent indicator value for these lake types (Gannon & Stemberger, 1978).



**Fig. 2.** The main factors determining the distribution of zooplankton assemblages.

Some species of Cladocera have wide ecological tolerance and are able to colonize various types of aquatic environment, whereas other taxa are more restricted to particular conditions and narrower ecological niches (Flössner, 1964). The distribution of many species of Chydoridae has been related to the physical structure (Chengalath 1982; Duigan & Kovach, 1994), water chemistry (Whiteside, 1970; Boronat *et al.*, 2001) and trophic state (Harmsworth & Whiteside, 1968) of lakes. The response of chydorids to anthropogenically-induced changes has enabled pseudofossils of cladocerans, and chydorids in particular, to be used widely in palaeolimnological studies to reconstruct trophic or acid conditions (Harmsworth & Whiteside, 1968; Whiteside, 1970; Brodersen *et al.*, 1998; Jeppesen *et al.*, 2001 a), to infer changes in macrophyte and fish communities (Jeppesen *et al.*, 2001 b) and to trace temperature changes (Duigan & Birks, 2000). To understand the role of chydorids as indicators of

change requires detailed knowledge of their distribution and ecology. Regional differences between chydorid assemblages need to be examined in order to assess European-wide applicability.

Fish predation directly influences pelagic predator-prey relationships (Brooks & Dodson, 1965). Fish usually reduce the number of zooplankton as well as their size-regime; the greater the pressure of fish predation, the more biased the size structure of the zooplankton community (Korhola & Rautio, 2001). Fish usually select larger prey, whereas with invertebrate predation, small-sized individuals are effectively removed (Brooks & Dodson, 1965).

Cladocera are known to be highly responsive to the substrata they inhabit (Flössner, 1964). Within a lake, Cladocera occur in both the offshore (pelagic) regions, where the families Daphniidae and Bosminidae predominate, and in the shallow littoral zone, where diverse members of the family Chydoridae are most abundant (Korhola & Rautio, 2001). For instance, lake-level fluctuations may induce changes in habitat composition suitable for different species of Cladocera by changing the relative proportions of littoral-pelagic habitats, and further changes within the littoral zone (Mueller, 1964). Many studies have recognized the important influence of lake depth on the cladoceran distribution (Whiteside, 1970; Korhola *et al.*, 2000).

*Ceriodaphnia* spp. tend to be more numerous in the plant-dominated littoral zones of lakes than in the pelagic zones (Flössner, 1964). *Chydorus sphaericus* tends to be abundant when macrophyte coverage is high, but is also common in association with cyanobacterial blooms in nutrient-rich lakes lacking submerged plants (Jeppesen *et al.*, 2001a).

In the pelagic zones of eutrophic temperate lakes and reservoirs, small-bodied cladoceran species such as *Bosmina* spp. and *C. sphaericus* are generally more abundant than large-bodied species (e.g. *Daphnia* sp.) (DeMott & Kerfoot, 1982). It is widely accepted that the pelagic zones of low productivity lakes tend to be dominated by large-bodied cladocerans and that the size of the dominant forms decreases with increasing trophic level (Pejler, 1975).

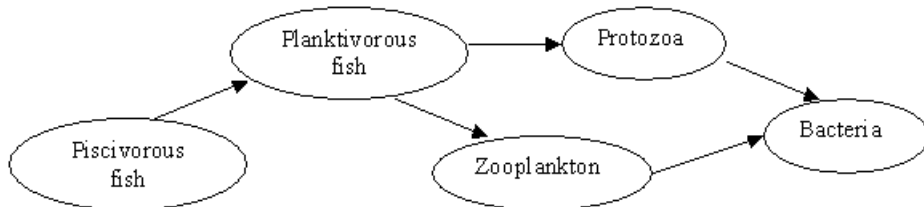
Eutrophication can have considerable impact on the composition and abundance of zooplankton species. Oligotrophic lakes generally display a low biomass comprising a great variety of species, while lakes in the “bloom” condition characteristic of advanced eutrophy exhibit a large biomass with fewer species (Gannon & Stemberger, 1978). Under conditions of nutrient enrichment, the average size of zooplankters often decreases as smaller species with simpler life histories and more rapid rates of reproduction appear in the plankton community (Gliwicz, 1969). Zooplankters, especially rotifers, primarily considered littoral species, often become abundant in the limnetic zone of eutrophic waters (e.g. *Brachionus*, *Euchlanis*, *Lecane*, *Lepadella*, *Trichocerca*) (Stemberger, 1974).

Calanoid copepods generally appear best-adapted to oligotrophic conditions while cladocerans and cyclopoid copepods are relatively more abundant in eutrophic waters. The ratio of calanoid copepods to cladocerans and cyclopoid

copepods appeared to be a good indicator of trophic conditions in the Laurentian Great lakes (Gannon & Stemberger, 1978).

## 2.2. Fish predation can determine the structure of a lake ecosystem

Zooplankton is the main food of fish larvae and fry in many aquatic systems (Meshiatti & Arcifa, 2002). Fish predation can have both direct and indirect effects on the entire lake food web (Fig. 3). Zooplankters are important prey during the first summer because mouth width seems to be the critical determinant of a fish's ability to handle large food items (Strelnikova & Ivanova, 1983; Naesje *et al.*, 1987). The young fish larvae feed initially on rotifers and copepod nauplii, but they soon also start to prey on cladocerans (Wang, 1994; Nandini & Sarma, 2000). The share of cladocerans in their diet grows gradually (Karjalainen, 1992); they begin to prefer larger cladocerans (e.g. *Leptodora*, *Diaphanosoma*, *Daphnia*) (Gannon, 1976; Herzig, 1995) and also copepods (Langeland, 1982). Phytoplankton can also be important as an initial food item for newly-hatched smelt larvae, as found in Norwegian Lake Mjøsa by Naesje *et al.* (1987).



**Fig. 3.** Effect of fish predation on the lake food web and microbial loop.

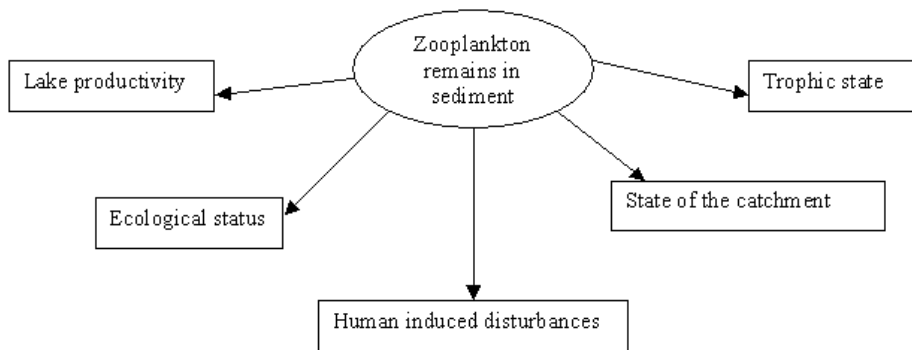
Predation by adult planktivorous fish and by the juveniles of all fish species may be the main determinant of the structure and abundance of zooplankton communities in lakes (Mills & Forney, 1983). Because of fish predation the density of large cladocerans (e.g. *Daphnia galeata*, *Leptodora kindtii*) usually decreases while the proportion of smaller species (e.g. *Bosmina longirostris*, *Ceriodaphnia* spp.) increases (Ohtaka *et al.*, 1996; Jeppesen *et al.*, 2001). Usually, predation by planktivorous fish mostly influences cladocerans, as the copepods are better-adapted to avoid predation (Bergman, 1990). In Lake Mjøsa the age-0 smelt feed mainly on copepods and cladocerans from mid-summer to autumn, with no strong preference for either of these groups (Naesje *et al.*, 1987). In Finnish lakes, age-0 smelt feed mainly on copepods, sometimes on

cladocerans, usually in proportion to their availability in the plankton (Karjalainen *et al.*, 1997). In Frederiksborg Slotsso (Denmark), where the diet of the entire roach and bream populations (all size-classes) was studied, the food ingested by 1–2-year old roach was mainly zooplankton (90% *Daphnia* and the rest composed of *Leptodora* and *Chydorus*) supplemented with detritus and benthos; the stomach of 3–4-year old bream contained almost equal amounts of benthos and zooplankton (*Alona* 50%, *Daphnia* 45% and *Leptodora* 5%), together with a substantial amount of detritus (Christoffersen & Bosselmann, 1997).

The predation effects cascade through the food webs and can be considered a major determinant of planktonic community dynamics (Huston, 1979). Alterations of the metazooplankton community structure may affect phytoplankton (Persson, 1997) and protozooplankton (Gilbert & Jack, 1993; Wickham, 1995; Jürgens & Jeppesen, 2000) communities, and change phytoplankton abundance and water clarity. Protozooplankton abundance and species composition can directly influence bacterioplankton (Beaver & Crisman, 1982; Güde, 1989; Gonzales *et al.*, 1990; Hall *et al.*, 1993). Increased grazing by pelagic zooplankton hiding from fish in macrophytes during the daytime (Timms & Moss, 1984), as well as the grazing by macrophyte-associated zooplankton species (Lauridsen *et al.*, 1996), has often been considered a major factor in suppressing phytoplankton biomass in macrophyte-dominated lakes. Nowadays the concept of a “grazing food chain” is supplemented by the concepts of a “microbial loop”, starting with bacteria consuming dissolved organic matter, and a “microbial food web”, in which small ciliates together with heterotrophic flagellates play a key role in linking pico- and nanoplankton to higher trophic levels (Azam *et al.*, 1983). The cascading effect of planktivorous fish on the microbial loop is still understudied. The role of fish is often neglected because it is difficult to assess their abundance and feeding rate. Riemann (1985) first showed experimentally that increases in planktivorous fish caused significant increases in heterotrophic nanoflagellate abundance. He attributed the increase to reduced predation from large cladoceran species. Subsequent enclosure experiments confirmed these early results (Christoffersen *et al.*, 1993; Markořova & Jeřek, 1993). Comparing two lakes with contrasting food web structures, Vaque & Pace (1992) found that the lake dominated by planktivorous fish contained a greater abundance of heterotrophic nanoflagellates than the lake dominated by piscivorous fish. An enclosure experiment carried out in a small oligotrophic lake on the Canadian Shield (Tzaras *et al.*, 1999) showed that fish alone had no significant effect on the abundance of bacteria and heterotrophic nanoflagellates. The effect of nutrient treatment was greater when fish were present. Müller-Solger *et al.* (1997) found in mesocosm experiments conducted in a mesotrophic lake that the total ciliate biovolume increased in the presence of planktivorous fish. However, the impact on ciliates was species-specific. Several studies have demonstrated that the addition of planktivorous fish increases rotifer abundance (e.g. Mazumder *et al.*, 1990; Lazzaro *et al.*, 1992).

## 2.3. Zooplankton remains in sediments indicate historical conditions in lakes

Human activities have increased erosion and the inflow of extra nutrients into lakes, disturbing their biological balance and causing eutrophication. Paleolimnological studies of plant and animal remains in lake sediments allow these past environmental changes to be back-tracked (Parise & Riva, 1982; Frey, 1986; Korhola & Rautio, 2001) (Fig. 4).



**Fig. 4.** By studying zooplankton remains in the sediments, we can learn about the historical changes in a lake ecosystem.

Cladoceran remains, which accumulate in lake sediments, are excellent research material. Cladocerans can grow only by periodically shedding their exoskeletons. The cast exoskeletons are rapidly disarticulated by biological activity into their component pieces: headshield, shell, post-abdomen, post-abdominal claws, antennules, antennal segments, mandibles and portions of trunk limbs. In addition, gamogenetic individuals can contribute ephippia, copulatory hooks and specialized headshields and post-abdomens. Different individuals generate different numbers of exoskeletons and hence of skeletal fragments, depending on how many times they moult before death. There are also differences among families, and even among species within the same family, in the preservation of chitin and of the various exoskeletal components, obviously controlled by biochemical differences that affect the ease of biodegradation. All skeletal parts, and gamogenetic individuals with ephippia, seem to be preserved quantitatively among the Bosminidae and Chydoridae, whereas the Sididae, Holopediidae, Daphniidae, Moinidae, Polyphemidae and Leptodoridae are variably represented by post-abdominal claws, sometimes with part of the post-abdomen still attached, antennal segments, mandibles, caudal spines and ephippia. Many of these parts are less highly differentiated morphologically than the shells and headshields, making it considerably more difficult to determine the species

involved. Such fragments are often very small and hence run a greater chance of being lost during processing of the sediments, especially if the residue is run through a sieve. The family Chydoridae is represented by the greatest number of species, most of which can be identified confidently from their abundant exoskeletal fragments in the sediments. The Bosminidae are also well-represented by exoskeletal fragments. The Daphniidae have proved difficult to identify from isolated post-abdominal claws, mandibles and ephippia (Frey, 1986).

As Cladocera are the only zooplankton group that preserves well in lake sediments, this group is most preferable for use in paleolimnological studies (Sarmaja-Korjonen, 2001). Cladoceran species have different ecological and climatic preferences (Duigan, 1992). Littoral as well as planktonic species occur in this group. Cladocera are sensitive to the changes of lake trophic status (Brodersen *et al.*, 1998). Such changes are not only the normal results of lake development processes, but may also result from an excess of nutrients, which may indicate human activity (Szeroczynska, 1998; Goslar *et al.*, 1999; Sarmaja-Korjonen & Alhonen, 1999). Increased accumulation of zooplankton and benthic chydorids in lake sediments might indicate enhanced productivity (Jeppesen *et al.*, 2001 a).

An increased trophic state leads to changes in zooplankton composition and these changes can be back-tracked by the responses of the cladoceran community, e.g. by a marked increase of the abundance of *Chydorus sphaericus* and *Bosmina longirostris* (Goslar *et al.*, 1999; Sarmaja-Korjonen, 2002). Although *C. sphaericus* is a littoral species, its increase does not definitively indicate an increasing littoral zone (Mezquita & Miracle, 1997). *C. sphaericus* may be 'planktonic' during Cyanobacteria blooms in eutrophic waters, so its increase may also indicate rising primary productivity of the lake (Sarmaja-Korjonen, 2002).

An increase of *B. longirostris* may indicate an increased trophic state (Jeppesen *et al.*, 1996; Szeroczynska 1998, 2002), while *B. coregoni* prefers lower-productivity waters (Balaga *et al.*, 2002).

Hofmann (1977, 1978a, b) and Günther (1983) found a succession of species in lake cores from northern Germany: *B. longirostris* was present throughout the postglacial period, along with a succession of *Eubosmina* species, from *E. longispina* to *E. kessleri* and then to *E. coregoni*. Typically, the *Eubosmina* species occurring early in the history of a lake were replaced completely by *B. longirostris* (Frey, 1986). Hofmann regards this succession of species as indicating progressive eutrophication of the lakes. In three Swiss lakes with annually laminated sediments – Zürichsee, St. Moritzersee and Baldeggersee – *B. (Eubosmina) longispina* seemed to be replaced by *B. longirostris* within a single year (Boucherle & Züllig, 1983). This kind of replacement has usually been interpreted as a result of eutrophication and possibly mediated by the selective predation of *Chaoborus* on the larger species of *Bosmina* (Frey, 1986).

In the Segeberger See, Hofmann (1978a) found that species preferring "clear-water lakes" (*Acroperus harpae*, *Camptocercus rectirostris*, *Eurycercus*

*lamellatus*, *Graptoleberis testudinaria*) were dominant in the early phase of the postglacial period, whereas species typical of “polluted lakes” (*Alona rectangularis*, *A. quadrangularis*, *Leydigia quadrangularis*, *L. acanthocercoides*, *Pleuroxus uncinatus*, *C. sphaericus*) were dominant in the upper postglacial sediments.

Numerous studies have shown that the abundance of large-bodied zooplankton in the pelagic zone decreases with increasing fish predation (Brooks & Dodson, 1965). Cladoceran size and *Daphnia* abundance were inversely related to the catch per unit effort (CPUE, calculated as number of fish net<sup>-1</sup> night<sup>-1</sup>) of planktivorous fish in mesotrophic-eutrophic Danish lakes. The abundance of *Daphnia* was unimodally related to TP and CPUE (Jeppesen *et al.*, 1996).

Several paleolimnological studies have revealed distinct changes in the composition of cladoceran assemblages in association with evidence of acidification (Fryer, 1980; Steinberg *et al.*, 1988; Korhola, 1992). Increasing acidity may cause a loss of acid-sensitive species, decline in species richness and changes in total cladoceran biomass and abundance (Korhola & Rautio, 2001). Reduced species richness and the disappearance of acid-sensitive planktoners such as *Daphnia longispina*, *Bythotrephes longimanus*, *Leptodora kindtii* and *Bosmina longirostris* was observed in acidified Norwegian lakes (Nilssen & Sandoy, 1990). The rapid natural acidification of Lake Pieni Majaslampi in southern Finland during the early Holocene was associated with the replacement of *B. longirostris* with *B. (Eubosmina) longispina* and an increase in the number of acid-tolerant chydorid species such as *Alonella excisa* and *Alona nana* (Korhola & Tikkanen, 1991).

## 2.4. Aims of the study

The aims of the present study were:

1. To assess the relationship between lake ecological quality and zooplankton (especially Chydoridae) assemblages (**I**, **II**).

Many scientific studies have evaluated zooplankton as an indicator of lake water quality. However, they have mostly been conducted on a local scale and fail to satisfy the growing need for Europe-wide applicability. Our studies on the role of zooplankton in shallow lake ecosystems assess the indicative value of zooplanktoners on both local (**II**) and pan-European (**I**) scales and provide a basis for further large-scale assessments.

2. To follow the effect of planktivorous fish predation on food web structure on the basis of the fish gut contents (**III**, **IV**).

Despite the growing number of publications on the planktonic food web structure, studies that consider the cascading effect of planktivorous fish on the microbial loop are still extremely scarce. The role of fish is often neglected because of difficulties in assessing their abundance and feeding

rate. Our goal was to study planktivorous fish feeding and food web dynamics simultaneously, estimating the actual food composition of planktivorous fish and their impact on food web structure.

3. To estimate the past impact of agriculture on lake water quality using zooplankton from lake sediment as a high-resolution proxy (V).  
Back-tracking past environmental changes in lakes using zooplankton remains in the sediments is still a novel approach. Such investigations are rare and in Estonia the present one is unique. Our main goal in this study was therefore to prove that zooplankton can be used as a suitable proxy for tracking past ecosystem changes in Estonian lakes with varved sediments.

### 3. STUDY AREA

In paper **I**, six shallow lakes (mean depth less than 3 meters) were sampled in each of Ireland, the United Kingdom, Sweden, Estonia, Denmark, the Netherlands, Germany, Poland, north-western Spain and eastern Spain. These lakes were chosen to cover a wide range of ecoregions and ecological qualities (high, good and moderate) and physicochemical conditions. The lakes in Estonia were Mullutu Suurlaht, Kaiavere, Prossa, Uljaste, Valguta Mustjärv and Võrtsjärv.

In paper **II**, chydorids were collected from Lakes Prossa and Kaiavere, which are shallow calcareous eutrophic lakes. The bottom of Lake Prossa is densely covered with charophytes, *Chara tomentosa* and *Nitellopsis obtuse*, while Kaiavere is a plankton-dominated lake.

In paper **III**, samples were collected from Lake Peipsi, a moderately eutrophic polymictic lake (Nõges et al., 2008). Lake Peipsi is well mixed by the wind; there is no stratification of temperature, O<sub>2</sub> or hydrochemical parameters during the ice-free period. The main commercial fishes in the lake are smelt, pikeperch, perch, bream, pike, ruffe and roach, and until the early 1990s there was also vendace.

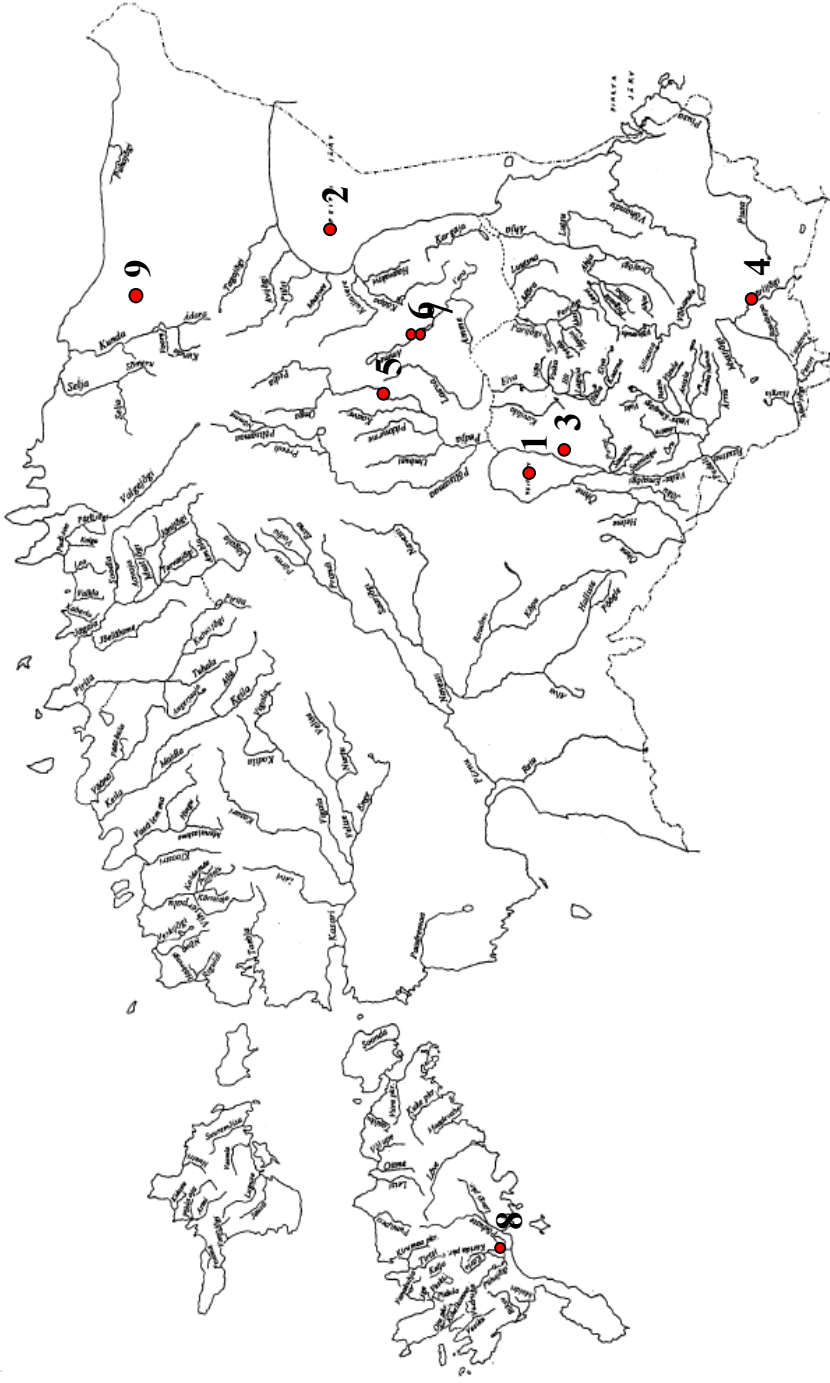
The experimental procedures in paper **IV** were conducted in four fishponds in Härjanurme fish farm (ponds A, B, C and D). Whitefish (*Coregonus lavaretus*) and pikeperch (*Sander lucioperca*) were introduced to ponds A and B. Only whitefish was introduced to pond C, and pond D had no planktivorous fish at all. All four ponds had been left dry over winter, filled with water again in the middle of April and emptied in October.

The studies in paper **V** were carried out in Lake Rõuge Tõugjärv, which is a small strongly stratified hard-water mesotrophic lake located in a kettle-hole depression in the primeval Rõuge valley in southern Estonia. The Rõuge area is an important prehistoric centre. Agricultural activity in the lake catchment has gradually increased since the 13<sup>th</sup> century, interrupted by cataclysms such as wars, famine and diseases.

Data about the lakes and ponds studied are summarized in Table 1. The locations of the lakes and ponds can be found in Figure 5.

**Table 1.** The main hydrobiological and chemical characteristics of the waterbodies studied.

Lake	Size, ha	Mean depth, m	TP, mg L <sup>-1</sup>	TN, mg L <sup>-1</sup>	Secchi depth, m	Phytopl. g m <sup>-3</sup>	Zoopl. g m <sup>-3</sup>	Main fish species
Peipsi	355800	8.3	0.04	0.7	1.5	1–125	3.1	Pike perch, bream, roach, perch
Rõuge Tõugjärv	4.2	7.6	0.02	1.5	1.7	–	–	Perch, pike, roach, ruffe
Prossa	33	2.2	0.0	1.2	2.7	1.4	0.8	Perch, roach, rudd, pike
Kaiavere	251	2.8	0.0	1.5	0.9	7.6	4.6	Bream, roach, perch, pike
Mullutu Suurlaht	5900	1.2	0.0	1.4	1.7	1.2	0.2	Ruffe, dace, ide, pike, roach
Uljaste	60	2.2	0.0	0.7	2	10	3.2	Perch, bream, roach, pike
Võrtsjärv	27000	2.8	0.0	1.2	0.8	15.6	0.6	Pike, eel, roach, bream, pike perch
Valguta Mustjärv	23	0.8	0.0	1.1	0.7	1.9	0.3	Crucian, pike, perch
Härjanurme pond A	6.9	1.6	–	–	0.6–1.8	1.3–4.0	0.1–18.3	Whitefish, pikeperch
Härjanurme pond B	6	1.6	–	–	0.5–1.8	0.9–4.1	0.1–45.2	Whitefish, pikeperch
Härjanurme pond C	2.4	1.6	–	–	0.7–1.8	0.3–3.2	0.04–43.5	Whitefish
Härjanurme pond D	7.2	1.6	–	–	0.6–1.7	0.1–2.7	1.4–25.1	–



**Fig. 5.** The locations of the lakes and ponds studied. 1 – Lake Võrtsjärv, 2 – L. Peipsi, 3 – L. Valguta Mustjärv, 4 – L. Rõuge Tõugjärv, 5 – Hārjanurme fish ponds, 6 – L. Kaiavere, 7 – L. Prossa, 8 – L. Mulutu Suurlaht, 9 – L. Uljaste.

## 4. MATERIALS AND METHODS

To investigate the chydorid species distribution (Paper I, II), samples were collected from the littoral zone in each lake at a depth of approximately 0.5 meter (Table 2). Stony substratum and any plant bed were sampled separately when possible. Replicate samples (3–5) were taken from each substratum. The samples were collected with sweep nets (mesh size 240  $\mu\text{m}$ ) swept over a 2-meter stretch of the lakebed, and were preserved in 90% industrial alcohol. Chydorids were identified and enumerated; species were identified according to Smirnov (1974).

For hydrochemical and plankton analyses (Paper II, Table 2), depth- and area-integrated samples were taken from the central parts of Lake Prossa and Lake Kaiavere. The sampling was carried out with a Ruttner sampler at 1-m depth intervals from the surface to the lake sediment. Samples were taken randomly from five stations in the lake and were pooled. For pelagic zooplankton, 10 l of this pooled water was filtered through a 48  $\mu\text{m}$  mesh and preserved with Lugol's solution. The biovolume of phytoplankton was measured using the Utermöhl (1958) technique. Zooplankton was counted in Bogorov's chambers. Hydrochemical analyses were performed using standard methods (Grasshoff *et al.*, 1982).

To determine the food consumption of a typical planktivorous fish (Paper III, Table 2), smelt samples were collected during summer and autumn 2003 with a bottom trawl (height 3 m, width 18 m, 10 mm knot-to-knot mesh size at cod-end), once a month from July to November. The total length (TL, to the nearest 1 mm) and total weight (TW, to the nearest 0.1 g) of each individual were measured by the method of Bagenal & Tesch (1978). The fish were preserved in 90% industrial alcohol. The numerical method (Hyslop, 1980) was used to analyse the fish digestive tracts. The digestive tracts were analysed on Petri dishes under a MBC-9 microscope with magnification  $\times 32$ –56.

The effects of fish on microbial dynamics in ponds were studied in Härjanurme fish farm (Paper IV, Table 2). The larvae were introduced to the ponds at similar densities shortly after hatching. Plankton sampling started on April 22 and the ponds were sampled approximately every third week until they were emptied in October. All plankton analyses were made from depth-integrated water collected at half-meter intervals using a Ruttner water sampler. Two subsamples were always taken from the same places: near the shore and at the midpoint of the pond. The total number of bacteria was determined by DAPI (4',6'-diamidino-2-phenylindole; Polysciences Inc) staining (Porter & Feig, 1980). The abundance was estimated by autofluorescence using a Zeiss Axiovert S100 epifluorescence microscope. For heterotrophic nanoflagellate counts the samples were fixed with buffered formalin, stained for 1–2 minutes with DAPI, filtered through 0.8- $\mu\text{m}$  pore-size black isopore filters and examined with an Olympus BX60 fluorescence microscope. Phytoplankton and ciliate subsamples were preserved and fixed with acidified Lugol's solution (0.5%

final concentration) and analysed using the standard Utermöhl technique (Utermöhl, 1958) with an inverted microscope. Metazooplankton was collected by filtering 10 l depth-integrated pond water through a plankton net (48 µm), fixed with Lugol's solution and counted under a stereomicroscope. The fish larvae and fry were sampled using a sweep-net or a gill-net. The fish were measured and weighed. They were preserved in ethanol and their whole digestive tract content was extracted and analysed.

To investigate cladoceran remains in the sediment (Paper V, Table 2), sediment cores were taken in winter 2000, using a freeze corer to acquire surface sediments and a Russian corer for deeper sediments. An age model of the sediments, based on careful documentation and counting of seasonal sediment laminae, was compiled. The varvochronology of the sequence was validated by radiometric measurements – the  $^{210}\text{Pb}$  method, with reference horizons of  $^{137}\text{Cs}$  and  $^{241}\text{Am}$  – and by the spheroidal fly-ash particle distribution in the sediments. Cladoceran remains were prepared for analysis according to standard methods (Frey, 1986). Sediment (1 ml) was heated in 100 ml 10% aqueous KOH for 30 minutes. The residue was sieved through a 40 µm mesh and at least 200 cladoceran remains were counted. Exotic *Lycopodium* spores were used to calculate the accumulation rates (AR; fossils  $\text{cm}^{-2} \text{yr}^{-1}$ ) of the biostratigraphic indicator.

**Table 2.** Summarized sampling routine in waterbodies studied.

Lake	Sampling time	Sampling frequency	Samples taken
Kaiavere	2000	in August	chydorids
	2000	monthly from April to October	phytoplankton
	2001	weekly from April to the middle of June	metazooplankton hydrochemical analyses
Prossa	2000	in August	chydorids
	2000	monthly from April to October	phytoplankton
	2001	weekly from April to the middle of June	metazooplankton hydrochemical analyses
Mullutu Suurlaht	2000	in August	chydorids
Uljaste	2000	in August	chydorids
Valguta Mustjärv	2000	in August	chydorids
Võrtsjärv	2000	in August	chydorids
Rõuge Tõugjärv	2000	once in winter	sediment cores
Peipsi	2003	once a month from July to November	smelt samples metazooplankton samples
Härjanurme pond A	2003	every third week from April to October	bacteria, phytoplankton, proto- and metazooplankton + fish (May-September)
Härjanurme pond B	2003	every third week from April to October	bacteria, phytoplankton, proto- and metazooplankton + fish (May-September)
Härjanurme pond C	2003	every third week from April to October	bacteria, phytoplankton, proto- and metazooplankton + fish (May-September)
Härjanurme pond D	2003	every third week from April to October	bacteria, phytoplankton, proto- and metazooplankton

## 5. RESULTS AND DISCUSSION

Paper I focuses on the description of chydorid assemblages from 66 European shallow lakes and presents data relating the assemblages to lake type and ecological quality. The aim of Paper II was to analyse the differences between two eutrophic shallow lakes. One of these lakes had a dense *Chara*-bed and became clear in summer, while the other was phytoplankton-dominated during the whole ice-free period. Paper III focuses on the feeding of 0+ smelt. Its main purpose was to describe the food consumption of a typical planktivorous fish in its first year of growth. Paper IV studies planktivorous fish feeding and the seasonal dynamics of bacteria, protozoa, phytoplankton and metazooplankton in four experimental fishponds. The hypothesis was that ponds in which planktivorous fish were present would contain fewer metazooplankton and the microbial loop would be more important. The converse situation would obtain in the pond without planktivorous fish. The aim of Paper V was to follow the impact of agriculture on water quality in Lake Rõuge Tõugjärv using Cladocera remains.

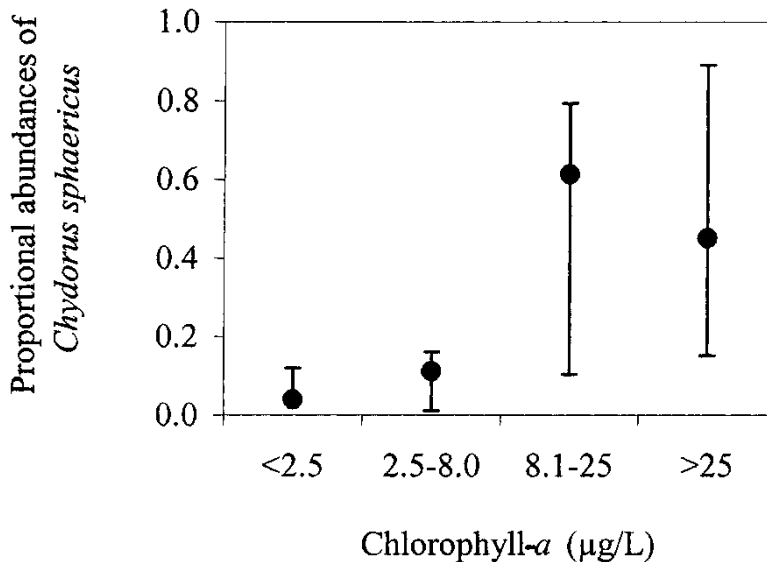
### 5.1. The relationship between lake ecological quality and zooplankton assemblages

To study the distribution of zooplankton and its application to ecological quality monitoring, chydorids were selected as the indicator group and studied in 66 shallow European lakes (I). The lakes were clustered according to similarities in the diversity of their chydorid assemblages and the dominance of particular species. Within each group of lakes, one species of chydorid was found to be more prevalent than others. *Alona rectangula* dominated in the two Spanish lakes (Group 1). *Graptoleberis testudinaria*, a species with a strong preference for macrophytes, dominated in one lake from Spain and one from the United Kingdom (Group 2). *Eurycercus lamellatus* showed a relatively high proportional abundance in one lake from Sweden and one from the U. K. (Group 3). Twenty-one lakes (in Estonia, Lake Võrtsjärv, L. Valguta Mustjärv, L. Uljaste, L. Mullutu Suurlaht and L. Kaiavere) were distinguished from the rest owing to the dominance of *Chydorus sphaericus* (Group 4). This species turned out to be the most common chydorid, occurring in 57 out of 66 lakes. All these assemblages generally had Shannon diversities less than 1. Group 5 comprised one lake from Ireland and one from Poland, both of which are clear water lakes and contained high proportions of *Alonella excisa*. In group 6 (one lake from each of Germany, Ireland, Poland and the U. K.), *Acroperus harpae* dominated, although the chydorid assemblages were quite species-rich. Group 7 comprised 26 lakes (in Estonia, Lake Prossa) and was characterized by diverse chydorid

assemblages, high species richness, high Shannon diversity indices and low dominance values.

Lakes split into low (<48°N), mid (48° N – 53° N) and high (>53° N) latitudes showed significant differences in their chydorid assemblages. *C. sphaericus*, *A. rectangulara* and *Alonella nana* dominated in the low latitude lakes. In the mid latitudes, *C. sphaericus* and *A. nana* were also important, with sub-dominance by *A. harpae*, *Alona affinis* and *A. excisa*. In the high latitudes, *C. sphaericus* was again the most dominant, but the rest of the assemblages comprised a diverse mix of *Alonella exigua*, *A. harpae*, *Pleuroxus truncatus*, *Alonopsis elongata*, *A. nana* and *Alona costata*.

Lakes grouped according to trophic status (TP < 10, 10–35, 36–100, > 100 µg/l; chl- $\alpha$  < 2.5, 2.5–8, 8.1–25, > 25 µg/l) also contained significantly different chydorid assemblages. This was mainly due to the proportional abundance of *C. sphaericus*, which tended to increase with trophic status (Fig. 6). The distribution of several other species varied according to lake nutrient concentrations: the distributions of *A. elongata* and *A. excisa* were skewed towards more oligotrophic lakes, while *Pleuroxus uncinatus* was mainly found in lakes with higher chlorophyll- $\alpha$  and TP concentrations.

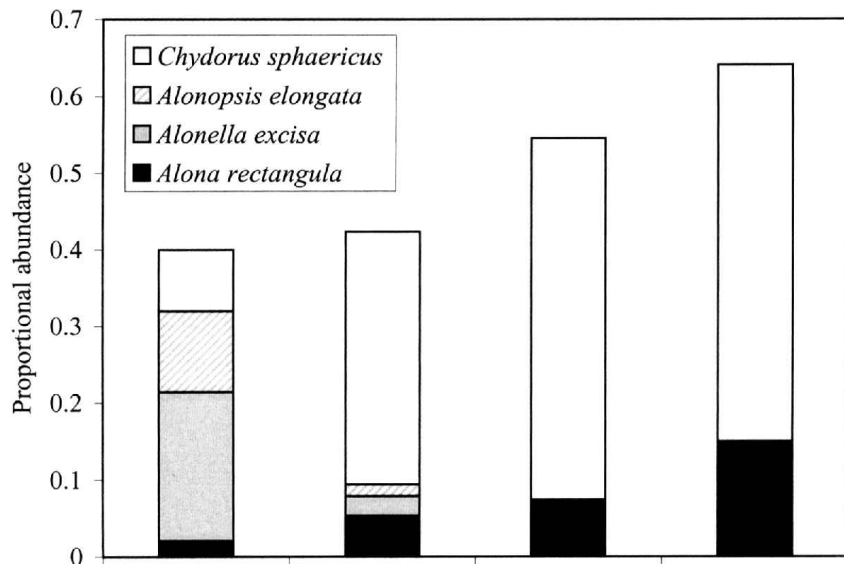


**Fig. 6.** Median proportional abundances of *Chydorus sphaericus* in the shallow European shallow lakes, grouped according to chlorophyll- $\alpha$  content. The whiskers represent the interquartile range; n = 59.

Several species showed marked preferences for either acidified or alkaline lakes. Species such as *A. elongata*, *A. excisa* and *Alona rustica* had higher proportional abundances in lakes with lower pH, while the proportional abundances of *A. rectangula*, *Chydorus latus* and *Pleuroxus aduncus* were higher in more alkaline lakes. *A. exigua* and *Alonopsis ambigua* displayed a preference for lakes with lower water temperature, while the proportional abundance of *A. nana* increased with water temperature.

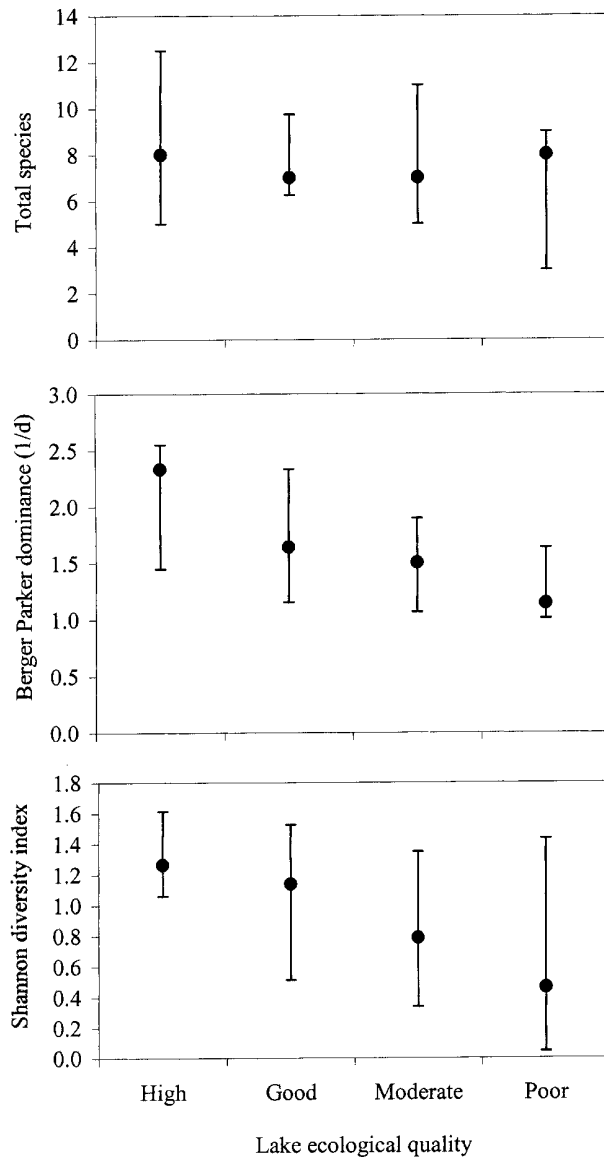
Species richness was negatively correlated with pH and positively correlated with latitude, although species richness declined steeply in the two most northerly lakes. Shannon diversity was correlated with latitude, Secchi depth and TP, although the relationship between TP and Shannon diversity appeared unimodal. Berger-Parker dominance also correlated with these three physiochemical variables.

In order to assess the relationship between chydorid assemblages and ecological quality, all 66 lakes were considered to represent high, good, moderate or poor ecological status. There were marked differences between the assemblages found in high quality lakes and those found in lakes classified as poor or moderate. This was mainly because high quality lakes were not generally dominated by *C. sphaericus* and had higher proportions of *A. excisa* and *A. elongata* than the poor and moderate quality lakes. *A. rectangula* was also less dominant in high and good quality lakes (Fig. 7).



**Fig. 7.** Average proportional abundances of *Alonopsis elongata*, *Alonella excisa*, *Alona rectangula* and *Chydorus sphaericus* in 66 lakes classified as being of high, good, moderate or poor ecological status.

While some trends between assemblage measures and ecological quality status were obvious (Fig. 8), it is clear that the relationship between chydorids and ecological quality is more apparent at species than at assemblage level.



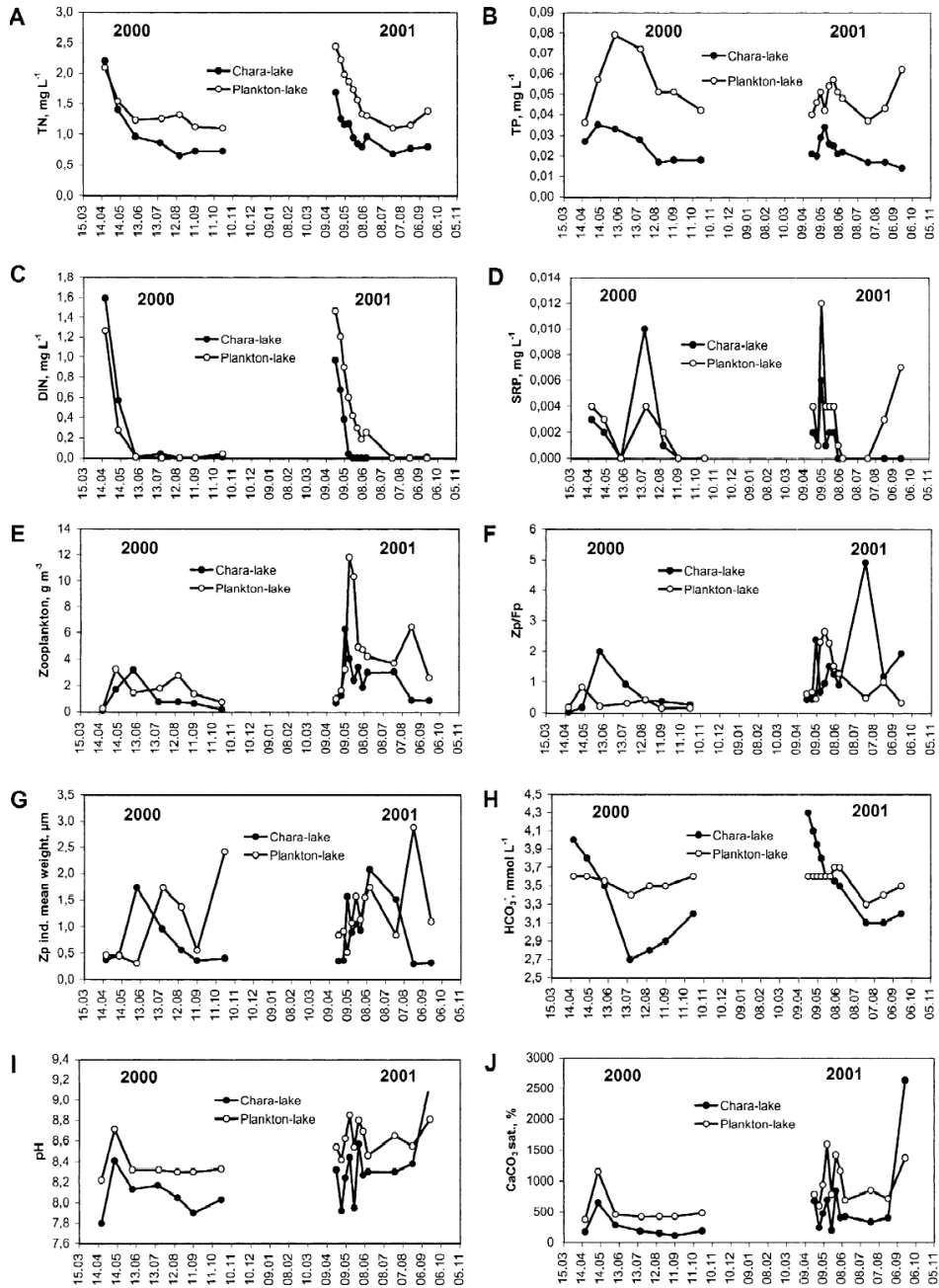
**Fig. 8.** Median species richness (top), Shannon diversity index (middle) and Berger-Parker index (bottom) of chydorid assemblages from European shallow lakes classified as being of high, good, moderate or poor ecological quality. The whiskers represent the interquartile range; n = 66.

To analyse more precisely the influence of lake ecological state on the zooplankton assemblages, two different shallow eutrophic lakes were examined: plankton-dominated L. Kaiavere and *Chara*-dominated L. Prossa (II).

Macrophytes can harbour high densities of phytoplankton that eat cladocerans, having a very strong influence on the lake food web. Our study showed that the biomass of the pelagic zooplankton in the *Chara*-lake (Fig. 9E) was almost always smaller than in the plankton-dominated lake. Also, the abundance of macrophyte-associated (MA) and sediment-associated (SA) hydroids was higher in the plankton-dominated lake. In the *Chara*-lake, MA was dominated by *Pleuroxus truncatus* and SA by *Acroperus harpae*, while *Chydorus sphaericus* was most numerous in both habitats in the plankton-dominated lake. In both years, the zoo- to phyto-plankton ratio (Zp/Pp) reached higher values in the *Chara*-lake than in the plankton-dominated lake (Fig. 9F). The individual mean weight of zooplankton peaked in the *Chara*-lake in June (caused by *Bosmina longirostris*) but in the plankton-dominated lake in autumn (Fig. 9G). The increased grazing pressure on phytoplankton by pelagic zooplankton hiding in macrophytes during the daytime (Timms & Moss, 1984), as well as grazing by macrophyte-associated zooplankton species (Lauridsen et al., 1996), has often been considered one of the most important factors controlling phytoplankton biomass in macrophyte-dominated lakes. In both years the individual mean size of zooplankton in the *Chara*-lake reached its maximum in June during the domination of *Bosmina longirostris*, which as an efficient grazer could initiate the clear-water period in this lake.

After a similar spring peak of phytoplankton in both lakes, the plankton biomass decreased and the water became clear in the *Chara*-lake, but the turbidity increased in the other lake together with the plankton biomass and the amount of suspended solids. In both lakes the spring peak of phytoplankton was caused by a mixed community consisting of diatoms, chlorophytes, chrysophytes, cryptophytes and dinophytes. After the spring peak the phytoplankton biomass declined in the *Chara*-lake, whilst in the plankton-lake the maximum phytoplankton biomass was achieved in autumn.

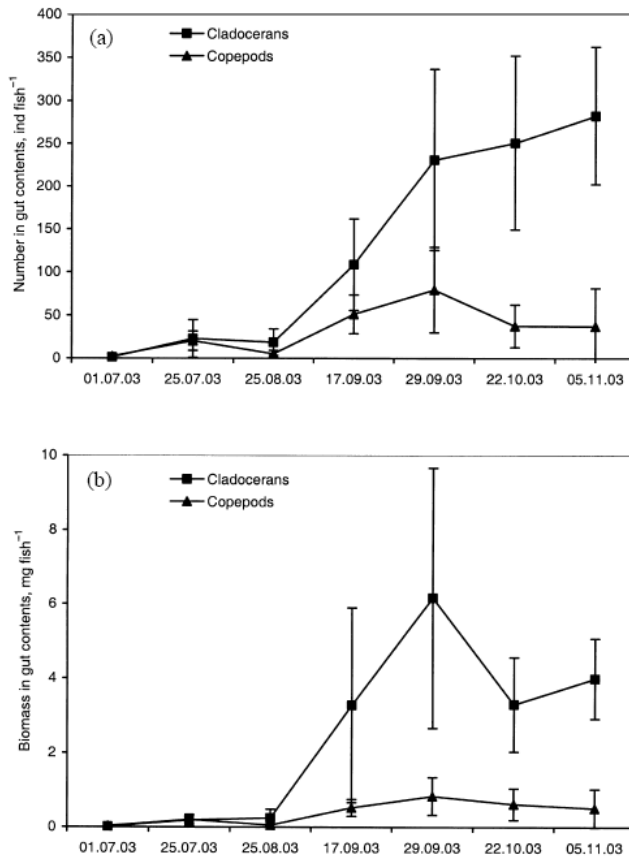
Towards autumn the Zp/Pp ratio as well as the mean individual Zp weight declined and remained at approximately the same level as in the plankton-dominated lake. Hence, zooplankton grazing probably initiated the clear-water phase, but other factors were involved in its maintenance.



**Fig. 9.** Seasonal dynamics of some chemical and biological parameters in the lakes studied. A – total nitrogen, B – total phosphorus, C – dissolved inorganic nitrogen, D – soluble reactive phosphorus, E – zooplankton biomass, F – zooplankton/phytoplankton biomass ratio, G – the mean individual weight of zooplankton, H – hydrocarbonate concentration, I – pH, J – calcite saturation level.

## 5.2. The effect of planktivorous fish predation on food web structure

To study the predation of planktivorous fish on the zooplankton we examined the feeding of 0+ smelt in L. Peipsi during a single year (III). Age 0+ smelt mainly consumed zooplankton (99%); chironomids, ostracods and diatoms were taken in negligible amounts. Presumably, smelt can continue feeding on zooplankton for quite a long time if there are enough large-bodied zooplankters in the lake so there is no need to shift to other food sources.



**Fig. 10.** Abundance (a) and biomass (b) of zooplankton groups in the gut contents of 0+ smelt in Lake Peipsi.

According to Ivlev's electivity index (Wootton, 1998), age 0+ smelt preferred cladocerans to copepods. Also, the biomass and numbers of cladocerans consumed were greater than those of copepods (Fig. 10). The preference for

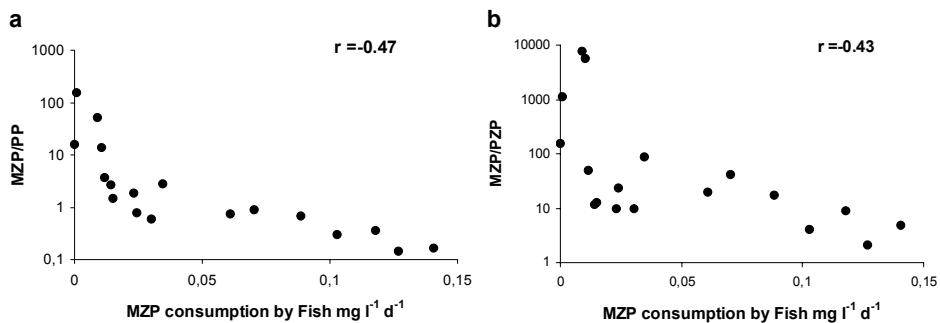
cladocerans over copepods may be because they are more easily captured and handled. At the beginning of July, smelt selected mainly large-bodied species and randomly ate smaller species; from July onwards, both large- and small-bodied species were taken. This may be due to predation pressure on zooplankton: in early summer there are fewer 0+ fish while large-bodied zooplankters are quite abundant. When the pressure increases the large-bodied zooplankters become less numerous and it is energetically preferable to consume both small- and large-bodied zooplankters.

We assessed the feeding impact of planktivorous fish on the seasonal dynamics of different plankton organisms in three natural food ponds (A, B, C) and compared the results with those from one pond without planktivorous fish (D). We hypothesized that in ponds where the planktivorous fish were present would contain lower numbers of metazooplankton and the microbial loop would be more important (IV).

Fish had a clear positive effect on protozoan abundances. Effectively removing larger grazers, they benefited the development of both flagellates and small ciliates. Many abundant ciliate species in our study ponds were small-sized picovores, which feed mainly on bacterioplankton (Zingel *et al.*, 2007) and are favourable prey for the larger copepods and cladocerans. Various studies conducted in enclosures have demonstrated that copepods and cladocerans can control the abundance of ciliates (Jürgens & Jeppesen, 2000; Gismervik, 2006). In our fishless pond we found a positive correlation ( $r=0.94$ ,  $p<0.01$ ) between the MZP and ciliates. In that pond the MZP biomass was largely made up of the predaceous *Leptodora kindtii*, which is known to prey mainly on small herbivorous cladocerans (Chang & Hanazato, 2004) and therefore favours the development of small-sized planktonic ciliates. We had predicted that in the absence of planktivorous fish the MZP density would be controlled from the bottom up and held at the equilibrium level of the carrying capacity of the habitat. But this proved only partly true in our case study. The MZP biomass was indeed much higher than in the other ponds, but we had predicted consequently lower phytoplankton and protozooplankton densities. In our fishless pond, *Leptodora kindtii* occupied the role of top predator and controlled the herbivorous zooplankton from the top. So the grazing pressure on the phytoplankton and protozooplankton was much lower. Bottom-up forces fixed the density of microheterotrophs; the abundance of bacteria depended on the top-down impact of grazing and was the lowest among the ponds studied.

We calculated the ratio of phytoplankton biomass to MZP biomass as an indicator of MZP grazing pressure on phytoplankton. This ratio was showed a significant positive correlation ( $r=-0.47$ ,  $p<0.01$ ) with the FFI (Fig. 11a). We also calculated the ratio of metazooplankton biomass to protozooplankton biomass as an indicator of classical food chain strength. This ratio was showed a significant negative correlation ( $r=-0.43$ ,  $p<0.01$ ) with the FFI (Fig. 11b), indicating that MZP removal by fish made the microbial food web more important.

Our study showed that planktivorous fish had a clear cascading effect on the microbial loop and controlled the system from the top. The food web dynamics described can be viewed as a classic example of ‘top-down’ and ‘bottom-up’ controls in aquatic systems. Planktivorous fish are known to switch from one prey item to another depending on their relative densities (e.g. Gliwicz, 2002), causing continual fluctuations in different prey item abundances. The seasonal dynamics of the food web was similar in ponds A, B and C but different in pond D. Different plankton groups were tied to each other and fluctuated markedly in the ponds where planktivorous fish were present. In contrast, the fishless pond showed very stable plankton dynamics.



**Fig. 11.** The biomass of metazooplankton (MZP) consumed daily by the planktivorous fish plotted against (a) the ratio of phytoplankton (PP) biomass to MZP biomass (PP/MZP), (b) the ratio of MZP biomass to protozooplankton (ciliates + heterotrophic nanoflagellates) biomass (MZP/PZP);  $p < 0.01$ .

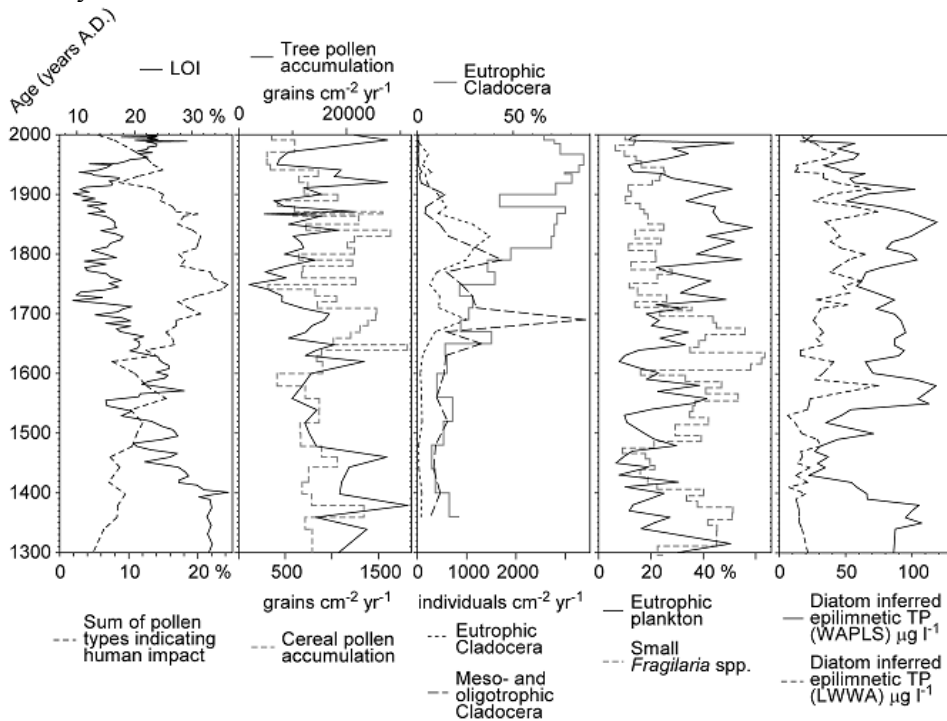
### 5.3. Estimating the historical changes in lake water quality using zooplankton remains in the sediment

To follow the impact of agriculture on water quality in L. Rõuge Tõugjärv we studied aquatic sub-fossils (including cladocerans) preserved in the varved lake sediment (V). Lakes, particularly those in fertile soils, may have been anthropogenically influenced for hundreds or thousands of years by agricultural activities and may have become more productive or disturbed. Human impact on these landscapes, starting with the development of primitive agriculture followed by forest clearance and more advanced land-use practices, has affected the lakes through various catchment processes. Thus, human-induced nutrient enrichment has caused major problems for aquatic ecosystems. Cladoceran remains in L. Rõuge Tõugjärv indicate the dominance of oligo- and mesotrophic taxa and overall low production during the period 1350–1650 A.D. Both diatom and cladoceran analyses show contemporaneous human-induced disturbance of the aquatic ecosystem (Fig. 12) and a clear change from oligo- and

mesotrophic Cladocera taxa to more eutrophic ones around 1650 A.D. A succession from a *Bosmina longispina*-dominated community to the one dominated by *Bosmina longirostris*, *Bosmina coregoni* and *Chydorus sphaericus* took place and the rate of accumulation of cladocerans was highest during 1650–1900 A.D.

A decline in the accumulation rates of eutrophic Cladocera and a recovery of mesotrophic cladoceran taxa show improved water quality from the 1900s onwards. In the second half of the 20<sup>th</sup> century, the relative proportion of eutrophic cladoceran species increased, although the absolute abundance of zooplankton remained low.

The lake recovered almost immediately after the collapse of Soviet-type agriculture in the early 1990s, and according to its diatom composition the modern lake is mesotrophic, with water quality similar to that of the 15<sup>th</sup> century.



**Fig. 12.** Combined summary diagram of Lake Rõuge Tõugjärv showing human-induced disturbance of the aquatic ecosystem and the surrounding vegetation. The diagram shows: down-core (in age-scale, years A.D.) curves of LOI (%) and pollen types indicating human impact (%); accumulation of tree pollen and cereals ( $\text{grains cm}^{-2} \text{ yr}^{-1}$ ); summary curve of Cladocera preferring eutrophic conditions (%), accumulation of oligo- and mesotrophic and of eutrophic Cladocera ( $\text{individuals cm}^{-2} \text{ yr}^{-1}$ ); relative abundance of eutrophic planktonic diatoms and sum of littoral *Fragilaria* spp. (%); diatom-inferred surface-water total phosphorus concentration ( $\mu\text{g l}^{-1}$ ) reconstructed using two different models.

## SUMMARY

1. Latitude, temperature, pH and nutrient status are the most important factors determining the distribution of chydorid assemblages of European shallow lakes. The species exhibiting the strongest relationship with ecological quality are *Chydorus sphaericus*, *Alonopsis elongata* and *Alonella excisa*. The proportional abundance of *C. sphaericus* shows a strong increasing trend with decreasing ecological quality. A concurrent increase in species such as *Alona rectangularis* and *Pleuroxus uncinatus* and a decrease in *A. excisa* and *A. elongatus* could also be linked with eutrophication.
2. Grazing of cladocerans on phytoplankton is responsible for initiating the increase in water transparency and development of clear-water status in the macrophyte-dominated lake in early summer, while other factors support the maintenance of the clear-water phase throughout the summer period.
3. Age 0+ smelt in Lake Peipsi mainly consumed zooplankton, especially cladocerans and copepods, but not rotifers. The taxa consumed were dominated by *Daphnia* sp., *Bosmina longirostris*, *Bosmina coregoni*, *Chydorus sphaericus*, *Eudiaptomus* sp., *Mesocyclops* spp. and cyclopoid copepods. Smelt preferred cladocerans to copepods.
4. The feeding impact of planktivorous fish on metazooplankton favoured protozooplankton and made the microbial food web relatively stronger. In situations where no planktivorous fish are present, the metazooplankton species composition (and especially the presence of large predaceous species) determines the food web structure.
5. Cladoceran remains proved to be a useful proxy for studying historical water quality changes in Lake Rõuge Tõugjärv. Changes in the cladoceran species composition in the varved lake sediment indicated historical changes in lake trophic status, revealing the human-induced eutrophication and recovery events during 1650–1990 A.D.

## SUMMARY IN ESTONIAN

### Zooplankton kui järvede ökoloogilise kvaliteedi ja kalade kisksurve indikaator

Zooplanktonil on järvede toiduahelates väga oluline roll. Zooplankterite võime tarbida autotroofseid vetikaid ning nende sobivus kalade toiduks määrab järve toitumisahelate efektiivsuse. Mida rohkem vetikatesse seotud orgaanilist ainet kaladeni jõuab, seda tõhusam on toitumisahel. Söömata zooplankterite osakesed akumuleeruvad aegamööda järvesetetes. Uurides settest võetud puursüdamikke, on võimalik saada järve zooplanktoni kohta ajas tagasiulatuvat teavet. Zooplanktoni kooslused on väga dünaamilised ning reageerivad kiiresti muutustele neid ümbritsevas keskkonnas. Seega saame me zooplanktonit uurides teavet nii järve praeguse kui ka ajaloolise ökoloogilise seisundi kohta.

#### Käesoleva töö eesmärkideks oli:

- leida seoseid järve ökoloogilise seisundi ja zooplanktoni koosluse struktuuri vahel;
- jälgida planktivoorsete kalade kiskluse mõju veekogu toiduahelatele, uurides kalade maosisaldisi;
- hinnata põllumajanduse ajaloolist mõju järve veekvaliteedile, kasutades selleks järvesetetes leiduvaid zooplankterite jäänuseid.

#### Selleks:

- uuriti hüdoriidide (*Chydoridae*) kooslusi 66 Euroopa madalas järves;
- analüüsiti zooplanktoni erinevusi eutroofsetes makrofüüdi- ja planktoni-järvedes;
- uuriti peipsi tindi (*Osmerus eperlanus*) noorjarkude toitumist Peipsi järves;
- võrreldi toiduahelaid tiikides, mis olid asustatud planktontoiduliste kaladega või kus sellised kalad puudusid;
- selgitati kalade kisksurve mõju mikroobsele lingule;
- jälgiti põllumajanduse ajaloolist mõju Rõuge Tõugjärve veekvaliteedile, kasutades selleks settes leiduvaid kladotseeride jäänuseid;

#### Töö tulemusena leiti, et:

- Hüdoriidide (*Chydoridae*) kooslusi mõjutavad Euroopa madalates järvedes kõige enam laiuskraad, temperatuur, pH ja toiteainete sisaldus. Liigid mis kõige paremini seostuvad veekvaliteediga on *Chydorus sphaericus*, *Alo-nopsis elongata* ja *Alonella excisa*. Veekogu halveneva ökoloogilise kvaliteedi ja *C. sphaericus*'e suhtelise arvukuse vahel on tugev positiivne seos. Samuti saab eutrofeerumisega siduda *Alona rectangula* ja *Pleuroxus unci-*

*natus*'e arvukuse tõusu, mis langeb kokku *Alona excisa* ja *A. elongatus*'e samaaegse kahanemisega.

- Kladotseeride toitumissurve fütoplanktonile suurendab makrofüüdi järves suve alguses vee läbipaistvust ja algatab “selge vee” perioodi. Samas tagavad teised faktorid suvekuudel “selge vee” perioodi püsimise.
- 0+ peipsi tint toitub Peipsi järves peamiselt zooplanktonist, põhiliselt aerjalgsetest ja vesikirbulistest. Domineerivad taksonid peipsi tindi toidus on *Daphnia* sp., *Bosmina longirostris*, *Bosmina coregoni*, *Chydorus sphaericus*, *Eudiaptomus* sp., *Mesocyclops* spp. ja sõudikuliste kopepodiidid. Peipsi tint eelistab selgelt vesikirbulisi aerjalgsetele.
- Kalade kisksurve metazooplanktonile soodustab protozooplanktoni arengut ning muudab mikroobse lünga suhteliselt tugevamaks. Olukordades, kus planktonitoidulised kalad puuduvad, määrab veekogu toiduahela struktuuri metazooplanktoni liigiline koosseis (eriti suurte röövtoiduliste vormide esinemine).
- Rõuge Tõugjärve setetest leitud vesikirbuliste jäänuseid saab kasutada uurimaks ajaloolis muutusi järve vee kvaliteedis. Vesikirbuliste liigilise koosluse muutused näitavad kätte ajaloolised nihked järve toitelisuses, osutades inimtegevuse mõjul alanud eutrofeerumistele ning tervenemistele ajavaheajal 1650–1990 m.a.j.

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## II Research history

### Research interests:

Zooplankton consumption by fish larvae, cladoceran remains in lake sediment as indirect indicator of eutrophication and fish predation.

### Publications:

de Eyto, E., Irvine, K., Garcia-Criado, F., Gyllstrom, M., Jeppensen, E., Kornijow, R., Miracle, MR., Nykanen, M., Bareiss, C., Cerbin, S., Salujoe, J., Franken, R., Stephens, D. & Moss, B. (2003). The distribution of chydorids (Branchiopoda, Anomopoda) in European shallow lakes and its application to ecological quality monitoring. *Archiv für Hydrobiologie*, 156(2), 181–202.

Nõges, P., Tuvikene, L., Feldmann, T., Tõnno, I., Künnap, H., Luup, H., Salujõe, J. & Nõges, T. (2003). The role of charophytes in increasing water

- transparency: a case study of two shallow lakes in Estonia. *Hydrobiologia*, 506(1–3), 567–573.
- Salujõe, J., Gottlob, H., Agasild, H., Haberman, J., Krause, T. & Zingel, P. (2008). Feeding of 0+ smelt *Osmerus eperlanus* in Lake Peipsi. *Estonian Journal of Ecology*, 57, 58–69.
- Salujõe, J., Zingel, P. & Paaver, T. (2009). The cascading effects of predation by planktivorous juvenile fish on the microbial loop. (submitted to *Limnologia*).
- Alliksaar, T., Heinsalu, A., Saarse, L., Salujõe, J. & Veski, S. (2005). A 700-year decadal scale record of lake response to catchment land use from annually laminated lake sediments in southern Estonia. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 29(1), 457–460.
- Laugaste, R., Haberman, J., Krause, T. & Salujõe, J. (2007). Significant changes in phyto- and zooplankton in Lake Peipsi in recent years: what is the underlying reason? Proceedings of the Estonian Academy of Sciences. *Biology, Ecology*, 56, 106–123.

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## II Teaduslik ja arendustegevus

### Peamised uurimisvaldkonnad:

Kalamaimude toitumine zooplanktonist, järve settes olevad vesikirbuliste jäänused kui eutrofeerumise ja kalade kiskluse kaudsed indikaatorid.

### Publikatsioonide loetelu:

- de Eyto, E., Irvine, K., Garcia-Criado, F., Gyllstrom, M., Jeppensen, E., Kornijow, R., Miracle, M.R., Nykanen, M., Bareiss, C., Cerbin, S., Salujoe, J., Franken, R., Stephens, D. & Moss, B. (2003). The distribution of chydorids (Branchiopoda, Anomopoda) in European shallow lakes and its application to ecological quality monitoring. *Archiv für Hydrobiologie*, 156(2), 181–202.
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## DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets.** Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet.** Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel.** Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe.** Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
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