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Significant changes in phyto- and zooplankton in L. Peipsi in recent years: what is the underlying reason?

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Abstract. The data for the vegetation periods (May–November) of 1997–2005 were used to analyse the dynamics of zooplankton and the most important phytoplankton groups in Lake Peipsi (Estonia). With some fluctuations, a continuous decline appeared in zooplankton abundance and biomass in those years. Since 1997 the share of cyanobacteria in phytoplankton biomass increased continuously: from 20% to 60% in L. Peipsi *s.s.*, and from 30% to 90% in the southern parts of the lake. In 2000, a heavy bloom of *Aphanizomenon flos-aquae* took place in October–November, and in the following year a significant decrease occurred in zooplankton, particularly in rotifers, and in phytoplankton biomass. In 2002, a very low water level, accompanied by high temperatures in August, caused a strong water bloom and fish kill. In the following years the zooplankton biomass (less than 1 g m^{-3}), particularly that of rotifers, was low. In the southern parts of the lake, the potentially highly toxic cyanobacterium *Microcystis viridis* started to dominate since August–September 2002. An appreciable concentration of cyanotoxins was detected in both lake parts in the same months in 2002. Possibly, this is one of the reasons for the significant decrease in the biomass of zooplankton, particularly rotifers. Another reason may be the growing grazing pressure of planktivorous fishes and fish fry on zooplankton.

Key words: zooplankton, cyanobacteria, toxins, fish predation.

INTRODUCTION

Investigations of zoo- and phytoplankton of L. Peipsi have been conducted (with some breaks) already for more than 40 years. During this time, plankton, particularly phytoplankton, has undergone several fluctuations in abundance and, to less extent, in the dominating species. However, the situation in the plankton community in recent years (after 2000) is totally different from that in earlier

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years. The present study is an attempt to analyse the circumstances that may be connected with significant changes in zooplankton. The possible factors affecting zooplankton are climatic conditions (water level and temperature), quantity and quality of food, presence of algal toxins, and fish predation.

The potential influence of water temperature on phyto- and zooplankton in L. Peipsi was analysed earlier (Laugaste & Haberman, 2005). All lake parts show an increasing trend of phytoplankton biomass (particularly cyanobacteria), which is most pronounced in the southern parts of the lake. We consider increasing eutrophication and climate warming to be possible driving forces for this phenomenon. Fluctuations in zooplankton biomass (average of the growing season) in the period 1965–2000 were usually not large. Our investigations did not show water temperature to be the main cause of yearly fluctuations or unidirectional changes in zooplankton biomass. A more likely cause is the indirect effect of temperature through phytoplankton as the food but also the suppressor of zooplankton in the form of cyanobacterial blooms. Extreme weather conditions in the previous autumn seem to have quite a strong impact on phytoplankton in the following year. The years with a low water level (1996 and 2002) and the year with very warm autumn months (2000) appear to have been crucial: after these years abrupt changes occurred in the plankton of the following year. The unusually warm October–November of 1996 and 2000 brought about a late heavy bloom of *Aphanizomenon flos-aquae* (L.) Ralfs and a scanty biomass of phytoplankton with even a shift in the dominant algal species in the following year. The mesotrophic diatom *Aulacoseira islandica* (O. Müller) Sim. disappeared from the lake and a decline of all other diatoms took place. The unfavourable influence of winter cyanobacteria on diatoms in the following spring was noted by Keating (1978, cited in Christoffersen, 1996). Thus the influence of the late autumn waterbloom in the following year is quite likely.

The amount of phytoplankton as an essential factor in the feeding of zooplankton in L. Peipsi is discussed in Haberman (2001), Laugaste et al. (2001), and Laugaste & Haberman (2005). The main criterion for the suitability of a food for zooplankton is evidently the size of food particles, up to 30–40 µm in diameter. However, zooplankters do not filter water in the sense of sieving, but particles of food are captured selectively (Wetzel & Likens, 1991; Jensen & Larsson, 2000). According to Nauwerck (1963), in L. Erken zooplankton prefer to eat small chrysophytes and cryptophytes, while small green algae with a thick cellulose shell are consumed in markedly smaller amounts. Nutrient limitation of green algae influences their cell walls, making them thicker, which probably reduces their digestibility, especially in P-limited cells (Ahlgren et al., 2000). On the other hand, Reinikainen & Repka (2003) stressed the high nutrient quality of cryptophytes, green algae, and diatoms. Consequently, chlorophytes are a common and important food item for zooplankton in many lakes. *Cryptomonas* serves as a high quality food according to Stutzman (1995). In L. Peipsi, cryptophytes, chlorophytes, and small centric diatoms seem to be an important source of food (Laugaste & Haberman, 2005), and food sources appear to be sufficient for zooplankton growth.

The aim of the present study was to find out possible causes of the change in zooplankton in recent years. Long-term data show that yearly fluctuations in water temperature are not correlated with the amount of zooplankton; nor is the amount of small algae (and bacteria) a limiting factor. We eliminate water temperature and food as the main factors and focus on fish predation and algal toxins.

STUDY SITE

Lake Peipsi *s.l.* (3558 km^2, mean depth 7.1 m, total phosphorus concentration (P_{tot}) 46.5 mg m^{-3}, total nitrogen concentration (N_{tot}) 687 mg m^{-3} as an average for the vegetation period of 1997–2005), located in Eastern Estonia, on the border of Estonia and Russia, consists of three parts with a different trophic state in each: moderately eutrophic clear-water L. Peipsi *s.s.*, highly eutrophic L. Pihkva (Pskov), and narrow L. Lämmijärv connecting the former two parts. Lake Pihkva is situated almost entirely within the borders of Russia and, with single exceptions, material from this lake was not available. Lake Peipsi is well mixed by the wind; there is no stratification of temperature, O_2, and hydrochemical parameters in the ice-free period.

Diatoms prevail in **phytoplankton** biomass in spring and autumn, and in some years also in summer. Besides the large filamental forms of *Aulacoseira islandica* (O. Müller) Sim., *A. granulata* (Ehr.) Sim., and *Stephanodiscus binderanus* (Kütz.) Krieger, unicellular centric species (genera *Cyclotella*, *Stephanodiscus, Cyclostephanos*) and, to a less extent, *Asterionella formosa* Hass., are abundant as well. Cyanobacteria yield maximum biomass in summer and autumn. A summer cyanobacterial bloom occurs every year, even with cool weather. The most conspicuous forms are *Gloeotrichia echinulata* (J. S. Smith) P. Richter in summer in L. Peipsi *s.s.* and *Aphanizomenon flos-aquae* (L.) Ralfs in autumn in the southern parts. The genera of *Microcystis* and *Anabaena* are also of importance, particularly since 2002.

The taxa that make up 20% or more of the total **zooplankton** number and biomass are considered the dominants. Along with the character species of oligo-mesotrophic waters (*Conochilus hippocrepis* (Schrank), *C. unicornis* Rousselet, *Kellicottia longispina* Kellicott, and *Bosmina berolinensis* Imhof), the dominants of L. Peipsi include also species preferring eutrophic waters (*Keratella cochlearis* (Gosse), *Daphnia cucullata* Sars, *Bosmina c. coregoni* Baird; sometimes, with respect to numbers, even *Anuraeopsis fissa* (Gosse) and *Keratella tecta* (Gosse)). The most important dominating zooplankters with respect to biomass are effective grazers of small algae: the calanoid *Eudiaptomus gracilis* (Sars) and species of the genera *Daphnia* (*D. cucullata*, *D. cristata* Sars, *D. galeata* (Sars)) and *Bosmina* (*B. berolinensis*, *B. gibbera* Schoedler, *B. c. coregoni*). In zooplankton, rotifers prevail in abundance throughout the year (on average 74% formerly, up to 50% lately), in biomass under the ice cover, and only in single cases in the vegetation period. Mass development of cladocerans starts in June when they make up about

30% of the total zooplankton biomass; they dominate in biomass in July (mainly the genus *Daphnia*) and account for about 50% of biomass in the autumn months (genus *Bosmina*). Copepods, particularly *Eudiaptomus gracilis* and species of the genus *Mesocyclops*, form about 35% of biomass during the whole year. The seasonal dynamics of zooplankton biomass is similar to that of water temperature, with a peak usually in midsummer. Also the biomass of herbivorous zooplankton commonly has a maximum in summer months (June–August).

MATERIAL AND METHODS

The basic material was collected monthly from the pelagial of the Estonian part of L. Peipsi (5–6 sampling sites) in the vegetation periods of 1997–2005. Samples from 15 stations over the whole area of the lake, including the southern part, L. Pihkva, were picked in August 2003 and 2005. The methods of collecting and treating samples are described in detail in Laugaste et al. (2001) and in Haberman (2001). Fish samples were collected with a bottom trawl (height 3 m, width 18 m, and codend of 10 mm mesh size knot-to-knot) from June 2003 to July 2005. The trawl was towed by a boat for 30 min per haul at a speed of 1 m s^{-1} and covered an area of about 0.3 ha. In total, 1197 individuals were measured (length and weight) of which 106 were examined for diet. The numerical method (Hyslop, 1980) was used in analysing fish digestive tracts. The number of individuals in each food category was recorded for all digestive systems and the total was expressed as a percentage of the total individuals in all food categories. Also the mean number of individuals per digestive system in each food category was calculated. The digestive tracts of fish were analysed on Petri dishes under microscope MBC-9 with magnification ×32–56. The hydrochemical samples were analysed in Tartu Environmental Researchers Ltd, Estonia. The program STATISTICS for Windows 7 was used for drawing figures.

RESULTS

In the 1990s the percentage of blue-green algae (cyanobacteria) in phytoplankton increased continuously, accounting for up to 80–90% of the total biomass in the southern lake parts (Fig. 1). A drop in the biomass was observed in 1997 and 2001, the years following a bloom of *Aphanizomenon flos-aquae* in November 1996 and 2000. The most important genera are all potentially toxic. The biomass of *Anabaena* species was fluctuating, with a high maximum in August 2002; *Aphanizomenon* reached a peak in October–November 1996 and 2000, and in the summer and autumn of 2001. *Gloeotrichia echinulata* peaked in L. Peipsi *s.s.* in July–August 2002. Drastic changes took place in the genus *Microcystis*: its growth began in summer 1999 in L. Lämmijärv (no data available from L. Pihkva), exceeding 20 g m^{-3} in July–September 2005 in the southern lake

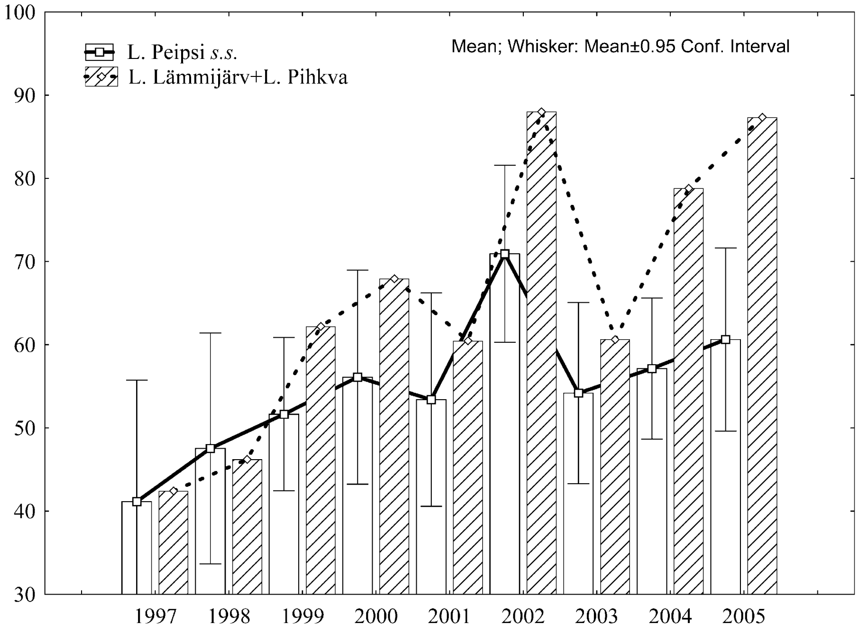


Fig. 1. Percentage of cyanobacteria in the phytoplankton biomass, average of July–September.

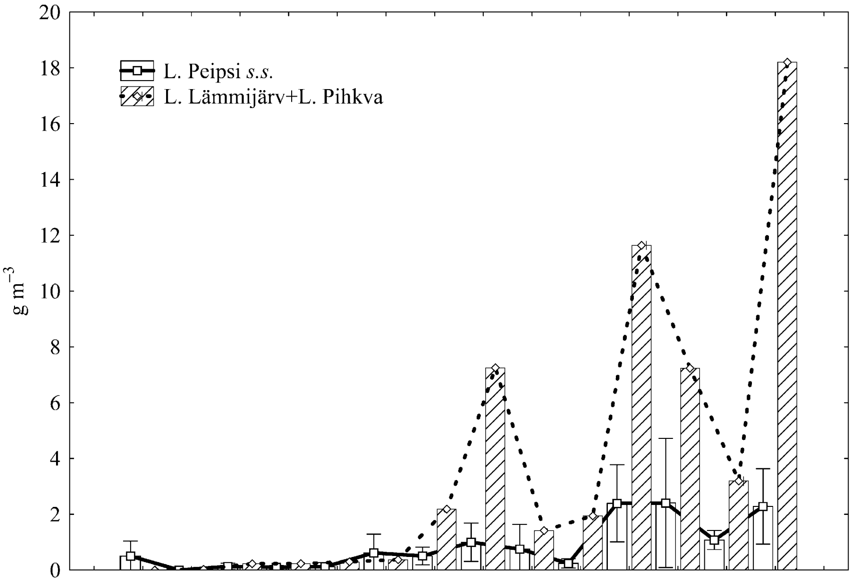


Fig. 2. Biomass of *Microcystis*, average of July–September.

parts (Fig. 2). *Microcystis viridis* (A. Braun) Lemm., one of the potentially most toxic species, prevailed. A less abrupt but obvious increase in blue-greens (mainly *Anabaena* species) was recorded from L. Peipsi *s.s.* Among the small algae (d < 40 µm) chlorophytes prevailed followed by cryptophytes and discoid diatoms (genera *Cyclotella*, *Stephanodiscus*, *Cyclostephanos*) and chrysophytes + haptophytes. A significant increase in the biomass of this group occurred in 1999 and 2004 (Fig. 3).

A significant decrease in the amount of zooplankton occurred since 2001 (Fig. 4a, b). The most drastic was the decline in rotifers: their abundance was 5–6 times lower in 2002–2005 than in the 1990s. In 1997–2005, the abundance and biomass of copepods decreased up to two times, the abundance and biomass of cladocerans almost two times (Fig. 5a, b). Thus, the percentage of rotifers in the total abundance and biomass diminished 2–3 times. It is noteworthy that not only the biomass of the filtrative zooplankton but also that of predators diminished since 2000, although for filtrators this decline was more essential (Fig. 6). The biomass of the genus *Daphnia* decreased since 2000 and had a minimum in 2005 with a seven times lower value than in 1999. *Daphnia cucullata* had its summer peak in July 2000, which was more than 10 times higher than in 2005. *Daphnia galeata* peaked in 2000 and showed minima in 2002–2003 and 2005. Also, the genus *Bosmina* had minima in 2003–2005 (Fig. 7). In the last three years, a drop

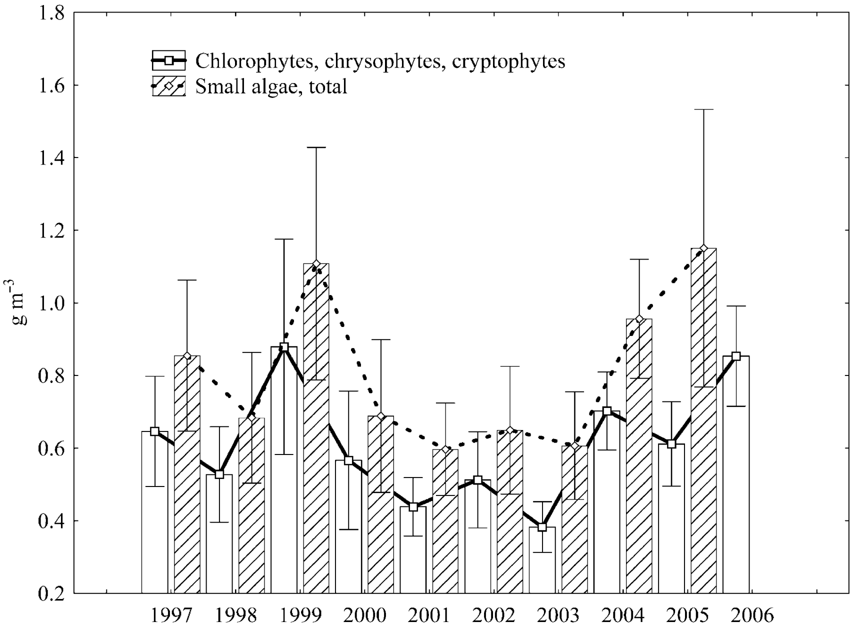


Fig. 3. Biomass of small algae (d < 40 µm), average of May–November in L. Peipsi (whole lake).

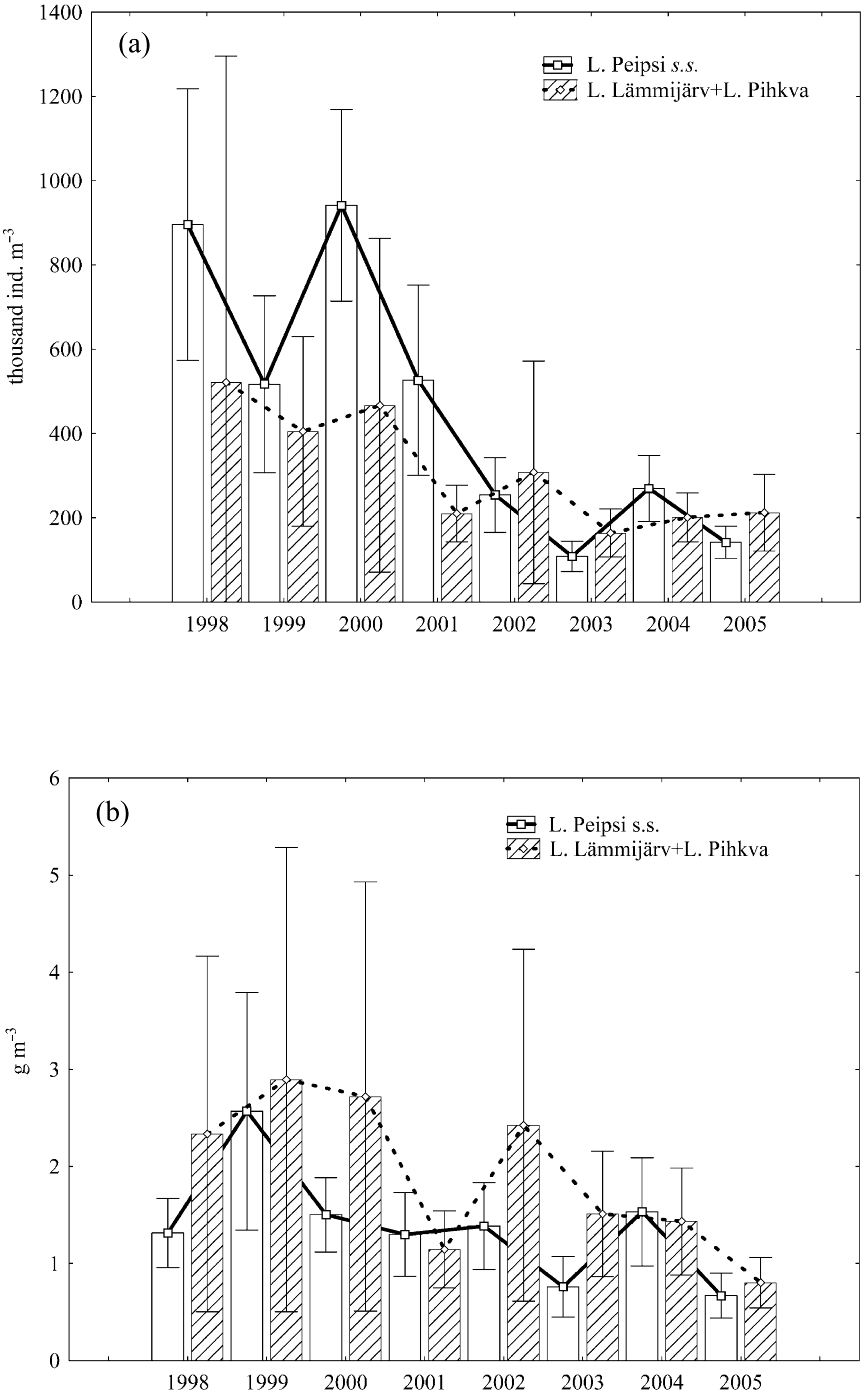
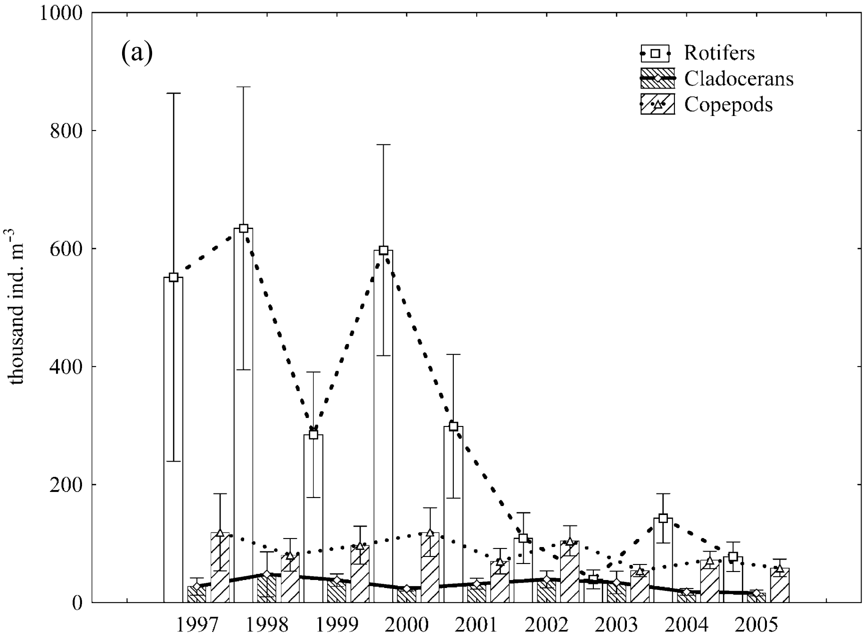


Fig. 4. Zooplankton abundance (a) and biomass (b) in two lake parts, average of May–November.



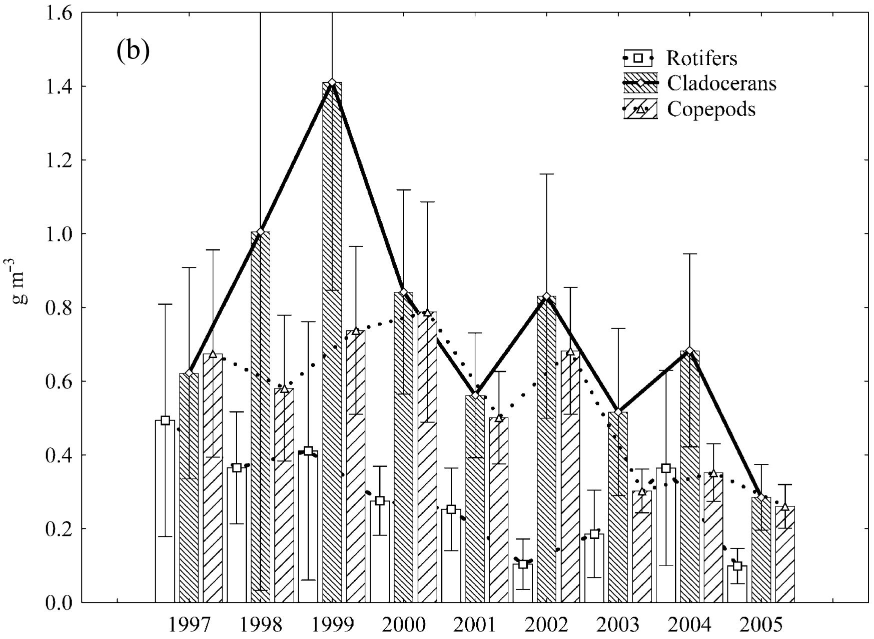


Fig. 5. Abundance (a) and biomass (b) of zooplankton groups in L. Peipsi (whole lake).

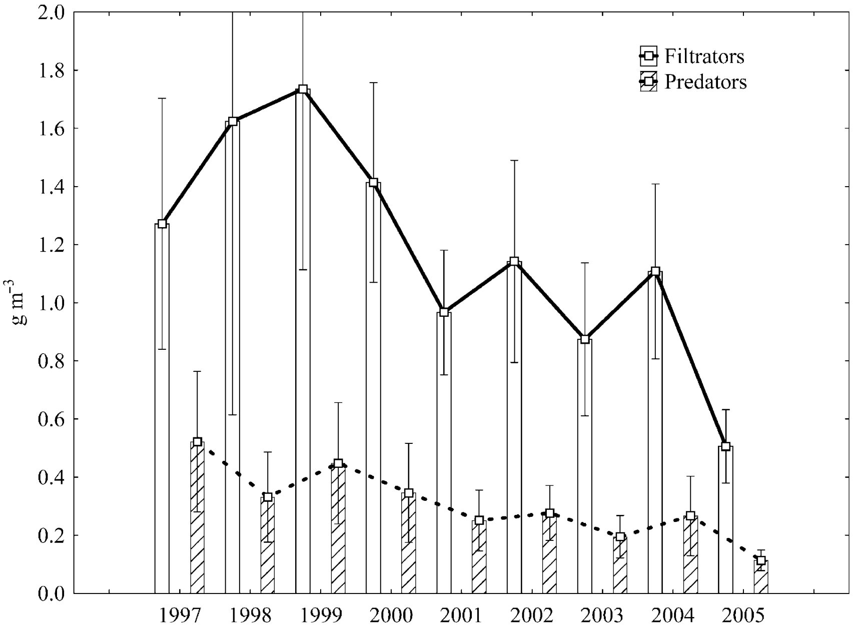


Fig. 6. Biomass of filtrative and predatory zooplankton in L. Peipsi (whole lake).

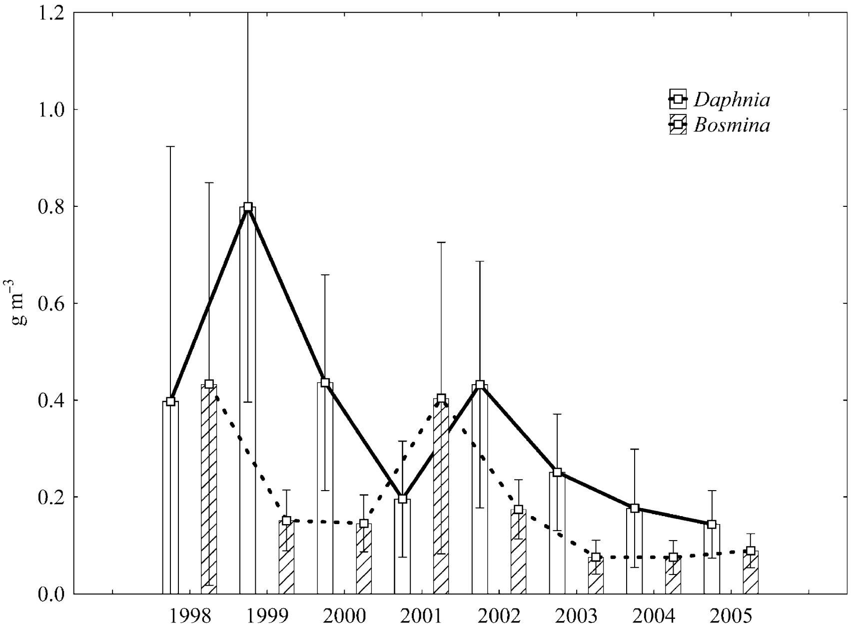


Fig. 7. Biomass of genera *Daphnia* and *Bosmina*, average of May–November in L. Peipsi (whole lake).

in *Eudiaptomus* was noted as well. Among rotifers, a notable decline was observed in the genera *Keratella*, *Conochilus*, *Kellicottia*, *Polyarthra*, *Synchaeta*, and *Anuraeopsis*.

The pressure of fish on zooplankton is usually the strongest in L. Peipsi in summer (June–August), in the period when all planktivores – lake smelt (*Osmerus eperlanus* m. *spirinchus* Pallas), fry of pikeperch (*Sander lucioperca* (L.)), perch (*Perca fluviatilis* L.), and roach (*Rutilus rutilus* L.) – feed on plankton. Pikeperch fry is added to the food for fish (mainly smelt) from August (Fig. 8). There was a very high pressure of fish on zooplankton in L. Peipsi in summer 2005 when large generations of pikeperch (20 times higher than in 2004!), smelt, and perch consumed them simultaneously. In August, when pikeperch began to consume smelt as food, a numerous perch generation continued to consume zooplankton. The number of 0+ pikeperch in bottom trawl catches (per haul) was 128 in 2004 and 2108 in 2005; the corresponding figures for smelt were 28 728 and 22 950. Earlier, numerous smelt generations occurred also in 2000 and 2002, and pikeperch generations in 1999 and 2001. Only the year 2003 was not productive as regards smelt, pikeperch, and perch. In 2003–2005 (July–November), the average proportion of cladocerans in zooplankton consumed by smelt was 37% and the proportion of copepods 12% (in July 2005 the corresponding figures were 8% and 42%, respectively). Of the consumed zooplankton in the digestive tract of pikeperch cladocerans made up 97.6% and copepods 2.4% in late July 2005; roach consumed up to 97% rotifers in June 2004, but 70% ephippia of daphniids in June 2003 (Fig. 9).

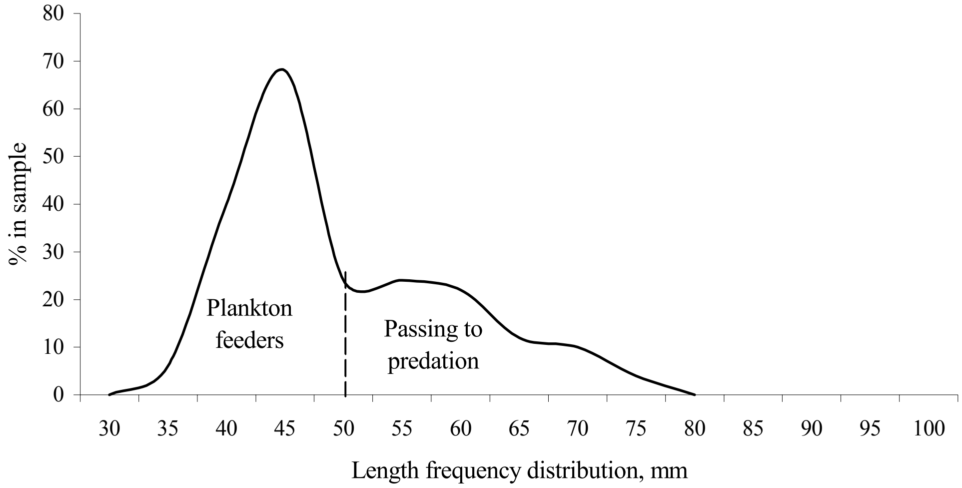


Fig. 8. Length frequency distribution of 0+ pikeperch in trawl, 27.07.05, $n = 210$.

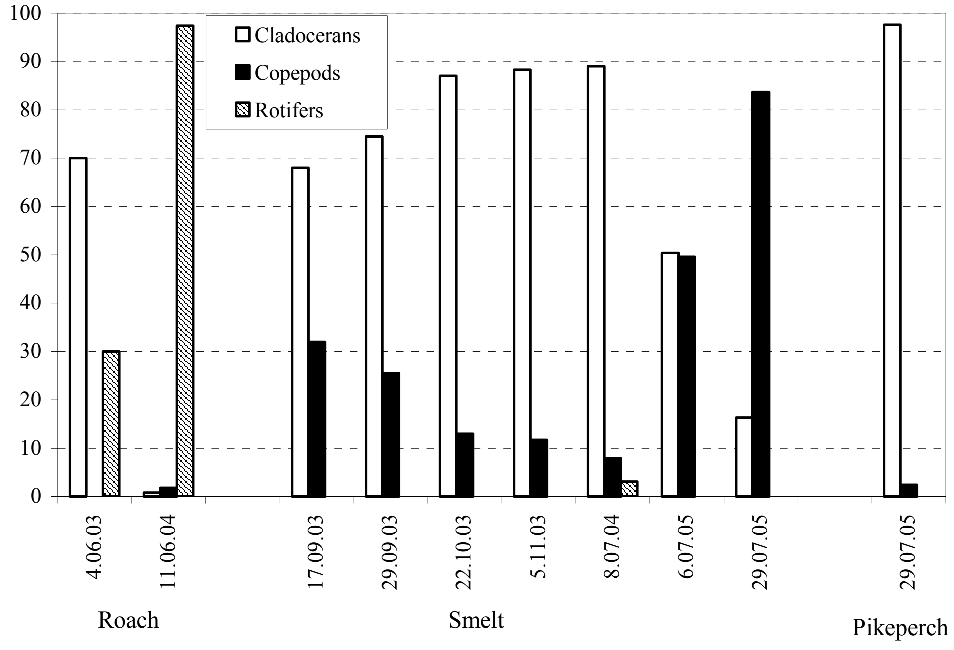


Fig. 9. Percentage of zooplankton groups in the consumed zooplankton in the digestive tract of smelt, roach, and pikeperch+perch.

DISCUSSION

According to experimental data, fish can cause a decrease in zooplankton (by consuming) as well as favour it via effects of nutrient cycling (Rejas et al., 2005). In recent years (since 1998–1999), both zooplankton abundance and biomass have shown an evident trend of decline in L. Peipsi. This trend characterizes all groups (rotifers, cladocerans, copepods, filtrators, predators) of zooplankton (Figs 4–6). The most confusing was the sharp decrease in the amount of rotifers, not especially vulnerable to fish predation. Rotifers are usually most dependent on the trophic state of the lake (May & O'Hare, 2005). A rise in the trophic state in the southern parts of L. Peipsi occurred in the late 1990s and in the 2000s (Milius et al., 2005); however, these changes do not seem to be the main reason for their decrease in this case as the drop in both the species preferring eutrophic conditions as well as the species preferring oligo-mesotrophic conditions showed a trend of slowing down. In moderately eutrophic L. Peipsi *s.s.*, a decrease in all zooplankton groups occurred as well. It is well known that zooplankters are subjected to a number of different factors of the aquatic environment, among them the most influential being fish predation (Maes et al., 2005; Hembre & Megard, 2005; Vijverberg & Vos, 2006). Not ignoring other possible influences, our opinion is that the changes in zooplankton (particularly cladocerans) in recent years were caused by fish predation. This is supported by the large amount of pikeperch fry in 1999, 2001, and especially in 2005, and that of smelt in 2000, 2002, 2004, and 2005. In L. Pyhäjärvi, large stocks of the planktivorous fish species vendace and smelt were accompanied by a reduction in cladoceran biomass and the practical disappearance of larger (>0.6 mm) cladocerans (Sarvala et al., 2000). In L. Peipsi, the highly productive fry of pikeperch in 1995 and 1997 (Afanas′ev et al., 2001) evidently influenced zooplankton biomass. Smelt has been among the most important fishes in L. Peipsi over time and it dominated in catches in 1994–2004. By today, its share in the total catch has decreased to 24.6%, while the share of pikeperch has increased up to 22.2% and that of perch up to 14.8% (Kangur et al., 2007). On the long-term scale, climate warming and continuing eutrophication have brought along a decline of cold- and clear-water fish species (vendace, smelt, whitefish) and an increase in the stock of pikeperch, which prefers warm and turbid water.

Planktivory by fish is a major factor determining the biomass, structure, and composition of both zooplankton and phytoplankton communities (Declerck & De Meester, 2003; Gliwicz et al., 2004; Rejas et al., 2005). However, several factors (nutrient deficit in phytoplankton, adaptive anti-predator responses of prey species, nutrient recycling) may weaken the links between the trophic levels. In the Bautzen reservoir, *Daphnia* consumption by fish aged 0+ accounted for up to 50% and even 100% of its mortality in the littoral zone. Yet due to gape-size limitation, fish aged 0+ did not feed on daphnids before June (Hülsmann et al., 1999). Analyses of the stomach content of rainbow trout showed that *Daphnia pulicaria* is a preferred prey. Feeding on *Daphnia* by trout is significantly higher compared to its abundance at the same time in the lake water (Hembre & Megard, 2005). Preferring larger food objects, fish feed first of all on cladocerans and copepods, clearly preferring cladocerans. The cladoceran *Bythotrephes longimanus* Leydig was the most preferred food object for whitefish in L. Peipsi in the 1970s (Gal′tsova & Denisenko, 1983). In L. Peipsi, smelt and vendace preferred large-sized *Daphnia galeata*, *Limnosida frontosa* Sars, *Bosmina berolinensis*, and *Leptodora kindti* (Focke), and the copepod *Eudiaptomus gracilis*; the populations of smelt, vendace, and young perch have consumed about 400 000 tonnes of cladocerans and copepods (among them 66% cladocerans) during a vegetation period (Ibneeva, 1983). According to Gal′tsova (1975), cladocerans, mainly *Daphnia longispina*, accounted for 59% and 92% in the food of smelt in L. Peipsi in July and September 1970, respectively. Also, our materials show a clear selectivity of fish for larger zooplankters (Fig. 9). Analysis of the content of the digestive tract of smelt, pikeperch, and roach shows that the food composition does not fully correspond to the zooplankton composition in the lake. Compared with zooplankton in the lake, the percentage of copepods in the content of the digestive tract of smelt was usually lower (about four times) than the corresponding percentage for the lake; the percentage of cladocerans consumed by fish was mostly higher (up to three times) than the corresponding percentage for the lake or similar to it. Pikeperch fry had consumed up to 98% cladocerans, while the percentage of this group in plankton was below 10. According to the data from 1966 (Tikhomirova, 1974), the food of smelt in L. Peipsi *s.s.* contained mainly copepods in May–June and in October, and cladocerans in July–September, which correlates with the seasonal dynamics of these groups. In L. Pihkva, warming up more quickly, cladocerans formed a major part of the food already in June. The author noted also the essential role of roach and perch fry in feeding on zooplankton, particularly cladocerans, in September 1966. Antipova (1991) observed that perch fry consumed copepods 55–64% in the first half of June, and cladocerans 70–90% in the second half in L. Pihkva in 1987. According to our data, only roach consumed small-bodied rotifers to an essential degree. In Lake Aydat (France), also young roach feed intensively on rotifers (Taleb et al., 1994). Evidently, in L. Peipsi predatory fishes have played an important role in the formation of the zooplankton community and in the decrease in the amount of cladocerans and copepods in recent years, particularly in 2005.

Adult egg-carrying female copepods and cladocerans and adult individuals of *Leptodora kindti* are rare in zooplankton samples of L. Peipsi. Also, the occurrence of *Bythotrephes longimanus*, *Limnosida frontosa*, and *Daphnia galeata* has become infrequent. The presence of eggs in the food cavity (which increases visibility for fish) was found to increase the smelt's selectivity for *Bosmina*, the adjusted mean selectivity index for egg-carrying females being twice as high as that for egg-free females (Gliwicz et al., 2004). *Leptodora kindti* serves as a favourite food item for fish (Herzig, 1995); on the other hand, in spite of its large body size but owing to its transparent body, *L. kindti* may be not vulnerable until the time of its first reproduction (Gliwicz et al., 2004).

In L. Peipsi, a direct relationship was established between zoo- and phytoplankton as the production of herbivorous zooplankton constituted 10.1% of primary production (Nõges et al., 1993). The biomass of small algae, including mostly green algae, increased abruptly in 1999 and 2004. The probable reason for this was the drop in zooplankton pressure. Cryptophytes did not display any pronounced increase at that time. The abundance of bacteria (main food objects of rotifers) had no definite trend in the investigation period (Fig. 10).

According to Tanner et al. (2005), the concentration of microcystins (5 types) in the open area of L. Peipsi *s.s.* at a depth of 30–50 cm is 50 $\mu g\ L^{-1}$ and the amount found in the region of the inshore accumulation of cyanobacterial mass was 1074 $\mu g\ L^{-1}$ at the beginning of September 2002. The dominating species were *Microcystis viridis* and *Anabaena circinalis*. In August 2003, the content of microcystins was about 1 $\mu g\ L^{-1}$ or less (prevailing species were *M. viridis*, *M. wesenbergii*, *Anabaena lemmermannii*); in July 2004 microcystins were not found (some *Anabaena* species were dominating). Compared with literature data (Christoffersen, 1996; Cronberg et al., 1999; Watanabe et al., 2000; Lindholm et al., 2003), the concentration of toxins in L. Peipsi appears to be very high in some cases, which definitely affects the biota. Several data indicate the harmful effect of toxins as well as bloom extracts on zooplankton (Christoffersen & Burns, 2000; Nandini, 2000; Agrawal et al., 2001; Ghadouani et al., 2003). Thorstrup &

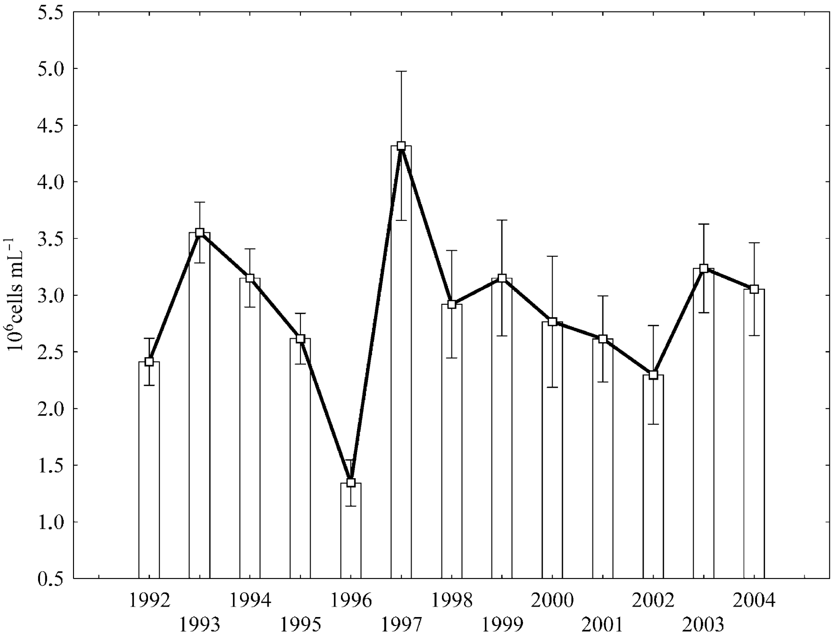


Fig. 10. Total abundance of bacteria, average of May–November in L. Peipsi (whole lake); monitoring data.

Christoffersen (1999) emphasized the existence of a negative correlation of the toxin concentration of *Microcystis* with the body length and fecundity of *Daphnia magna*. They also noted that microcystins can accumulate in *Daphnia* and in this way be transferred to the higher trophic levels of the food web. According to a review article of Christoffersen (1996), there are large species-specific differences between zooplankton species (as well as differences between different stages of life) in response to various toxins. Toxins may affect all organisms whether or not they consume algae. Slow-growing species appear less sensitive to the toxic *Microcystis* than fast-growing species (Ferrão-Filho & Azevedo, 2000). According to Gilbert (1994), the reproduction of four tested rotifer species was inhibited at anatoxin concentrations of 0.2–5 µg mL^{-1}. This author stresses that rotifers are the most sensitive zooplankton group and the sensitivity depends on the body weight of the organism. Thus, taking into consideration the scanty data on microcystin concentrations in L. Peipsi, toxic cyanobacterial blooms are among the probable causes that induced the drastic decline of rotifers and, to a less extent, of cladocerans and copepods in the lake.

What is the reason for the increase in *Microcystis* biomass in recent years? According to Blomquist et al. (1994, cited in Reynolds & Petersen, 2000), NH_4 is a key regulating factor causing dominance of non-nitrogen-fixing cyanobacteria. Wilk-Wozniak & Ligeza (2003) emphasized the relationship of cyanobacteria with water potassium content. In L. Peipsi, the concentration of ammonia even decreased significantly from 2000 onwards while a slight increase was observed in potassium. The increase in the P_{tot} content and the decrease in the N : P mass ratio (from 14 in 1992–1999 to 10 in 2000–2005 as an average of the growing season) occurred in the same period. This can explain the increasing dominance of cyanobacteria but not the growing importance of *Microcystis*. However, the about twofold increase in the Mg content in this period is noteworthy, although the effect of this process on phytoplankton remains unknown. In the opinion of Komárková et al. (1995), *Aphanizomenon* occurs only in the presence of large daphnids, and *Microcystis* replaces it after the large filter feeders have been removed. Can this fact be connected with the increasing domination of *Microcystis* in the southern parts of L. Peipsi?

A heavy kill of fish, particularly of smelt, occurred in several earlier hot summers (Kangur et al., 2005). The last fish kill in August 2002 damaged most perciids (ruffe, pikeperch, perch). Besides O_2 depletion and elevated ammonia, cyanotoxins may have played a role in this process. Zooplankton abundance decreased more than two times during the cyanobacterial bloom in August, with rotifers decreasing three times, cladocerans about four times, and copepods 1.7 times. The abundance of *Daphnia* species diminished 3.7 and that of *Bosmina* 2.7 times. Various species of rotifers decreased 6.5–13 times, the effect of toxins being evidently the main reason for this.

Thus we can suggest that the main reason for the decline in larger zooplankton groups, cladocerans and copepods, seems to be the pressure of fish fry and planktivorous smelt, but the effect of toxins cannot be excluded either; the main cause of the drastic drop in rotifers is probably toxic phytoplankton.

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REFERENCES

Afanas′ev, E. A., Koncevaya, N. Y., Sazonova, E. A. & Severin, S. O. 2001. Condition of the stock and industry of pikeperch in L. Pskovsko-Chudskoe. In *Materials of International Conference. Reports and Abstracts*, vol. 1 (Slinchak, A. I., Lebedeva, O. A. & Kochetkova, M. T., eds), pp. 161–163. Pskov (in Russian).

Agrawal, M. K., Bagchi, D. & Bagchi, S. N. 2001. Acute inhibition of protease and suppression of growth in zooplankter, *Moina macrocarpa*, by *Microcystis* blooms collected in central India. *Hydrobiologia*, **464**, 37–44.

Ahlgren, G., Hyenstrand, P., Vrede, T., Karlsson, E. & Zetterberg, S. 2000. Nutritional quality of *Scenedesmus quadricauda* (Chlorophyceae) grown in different nitrogen regimes and tested on *Daphnia*. *Verh. Internat. Verein. Limnol.*, **27**, 1234–1238.

Antipova, L. F. 1991. Ecology of the feeding of ruffe and perch in early stages of ontogenesis in L. Pskov. In *Abstracts of the 23rd Conference of Baltic Waterbodies* (Kutuzov, A. M. et al., eds), pp. 13–14. Petrozavodsk (in Russian).

Christoffersen, K. 1996. Ecological implications of cyanobacterial toxins in aquatic food webs. *Phycologia*, **35**, 42–50.

Christoffersen, K. & Burns, C. W. 2000. Toxic cyanobacteria in New Zealand lakes and toxicity to indigenous zooplankton. *Verh. Internat. Verein. Limnol.*, **27**, 3222–3225.

Cronberg, G., Annadotter, H. & Lawton, L. A. 1999. The occurrence of blue-green algae in Lake Ringsjön, southern Sweden, despite nutrient reduction and fish manipulation. *Hydrobiologia*, **404**, 123–129.

Declerck, S. & De Meester, L. 2003. Impact of fish predation on coexisting *Daphnia* taxa: a partial test of the temporal hybrid superiority hypothesis. *Hydrobiologia*, **500**, 83–94.

Ferrão-Filho, S. A. & Azevedo, S. M. 2000. Effects of unicellular and colonial forms of toxic *Microcystis aeruginosa* from laboratory cultures and natural populations on tropical cladocerans. *Aquat. Ecol.*, **37**, 23–35.

Gal′tsova, M. Z. 1975. On the feeding of smelt in L. Chudskoe (Peipsi). In *Raw Material Resources of L. Pskovsko-Chudskoe and Their Rational Utilization*, pp. 123–127. Lenizdat, Pskovskoe otdelenie (in Russian).

Gal′tsova, M. Z. & Denisenko, A. I. 1983. Selective feeding of vendace of L. Chudskoe (Peipsi). In *Abstracts of 21st Scientific Conference on Research into Waterbodies of the Baltic Republics and Byelorussia*, vol. 2, pp. 117–118. Pskov (in Russian).

Ghadouani, A., Pinel-Alloul, B. & Prepas, E. E. 2003. Effects of experimentally increased cyanobacterial blooms on crustacean zooplankton communities. *Freshwater Biol.*, **48**, 363–381.

Gilbert, J. J. 1994. Susceptibility of planktonic rotifers to a toxic strain of *Anabaena flos-aquae*. *Limnol. Oceanogr.*, **39**, 1286–1297.

Gliwicz, Z. M., Jawiński, A. & Pawlowicz, M. 2004. Cladocera densities, day-to-day variability in food selection by smelt, and the birth-rate compensation hypothesis. *Hydrobiologia*, **526**, 171–186.

Haberman, J. 2001. Zooplankton. In *Lake Peipsi. Flora and Fauna* (Pihu, E. & Haberman, J., eds), pp. 50–68. Sulemees Publishers, Tartu.

Hembre, L. K. & Megard, R. O. 2005. Timing of predation by rainbow trout controls Daphnia demography and the trophic status of a Minnesota lake. *Freshwater Biol.*, **50**, 1064–1080.

Herzig, A. 1995. *Leptodora kindti*: efficient predator and preferred prey item in Neusiedler See, Austria. *Hydrobiologia*, **307**, 273–282.

Hülsmann, S., Mehner, T., Worishka, S. & Plewa, M. 1999. Is the difference in population dynamics of *Daphnia galeata* in littoral and pelagic areas of a long-term biomanipulated reservoir affected by age-0 fish predation. *Hydrobiologia*, **408/409**, 57–63.

Hyslop, E. J. 1980. Stomach content analysis – a review of methods and their application. *J. Fish. Biol.*, **17**, 411–429.

Ibneeva, N. I.1983. Exploitation of food resources by planktophagous fishes in Lake Peipsi-Pihkva. *Sbornik nauchnykh trudov GosNIORKh*, **209**, 44–50 (in Russian).

Jensen, K. H. & Larsson, P. 2000. Experimental field and laboratory tests of food search in *Daphnia pulex*. *Verh. Internat. Verein. Limnol.*, **27**, 1795–1802.

Kangur, K., Kangur, A., Kangur, P. & Laugaste, R. 2005. Fish kill in Lake Peipsi in summer 2002 as a synergistic effect of a cyanobacterial bloom, high temperature, and low water level. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **54**, 67–80.

Kangur, A., Kangur, P., Kangur, K. & Möls, T. 2007. The role of temperature in the population dynamics of smelt *Osmerus eperlanus eperlanus* m. *spirinchus* Pallas in Lake Peipsi (Estonia/Russia). *Hydrobiologia* (in press).

Komárková, J., Vyhnálek, V. & Kubečka, J. 1995. Impact of fishstock manipulation on the composition of net phytoplankton in the Římov Reservoir (Czech Republic). *Wat. Sci. Technol.*, **32**(4), 207–216.

Laugaste, R. & Haberman, J. 2005. Seasonality of zoo- and phytoplankton in Lake Peipsi as a function of water temperature. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **54**, 18–39.

Laugaste, R., Nõges, P., Nõges, T., Yastremskij, V. V., Milius, A. & Ott, I. 2001. Algae. In *Lake Peipsi. Flora and Fauna* (Pihu, E. & Haberman, J., eds), pp. 31–49. Sulemees Publishers, Tartu.

Lindholm, T., Vesterquist, P., Spoof, L., Lundberg-Niinistö, C. & Meriluoto, J. 2003. Microcystin occurrence in lakes in Åland, SW Finland. *Hydrobiologia*, **505**, 129–138.

Maes, J., Tackx, M. & Soetaert, K. 2005. The predation impact of juvenile herring *Clupea harengus* and sprat *Sprattus sprattus* on estuarine zooplankton. *Hydrobiologia*, **540**, 225–235.

May, L. & O'Hare, M. 2005. Changes in rotifer species composition and abundance along a trophic gradient in Loch Lomond, Scotland, UK. *Hydrobiologia*, **546**, 397–404.

Milius, A., Laugaste, R., Möls, T., Haldna, M. & Kangur, K. 2005. Water level and water temperature as factors determining phytoplankton biomass and nutrient content in Lake Peipsi. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **54**, 5–17.

Nandini, S. 2000. Responses of rotifers and cladocerans to *Microcystis aeruginosa* (Cyanophyceae): a demographic study. *Aquat. Ecol.*, **34**, 227–242.

Nauwerck, A. 1963. Die Beziechungen zwischen Zooplankton und Fytoplankton im See Erken. *Symb. Bot. Uppsal.*, **17**(5), 1–153.

Nõges, T., Haberman, J., Timm, M. & Nõges, P. 1993. The seasonal dynamics and trophic relations of the plankton components in Lake Peipsi (Peipus). *Int. Rev. Hydrobiol.*, **78**(4), 513–519.

Reinikainen, M. & Repka, S. 2003. Phenotypic plasticity in life-history traits and feeding appendages in two species of *Daphnia* fed a natural phytoplankton assemblage. *Aquat. Ecol.*, **37**, 409–415.

Rejas, D., Declerck, S., Auwerkerken, J., Tak, P. & de Meester, L. 2005. Plankton dynamics in a tropical floodplain lake: fish, nutrients, and the relative importance of bottom-up and top-down control. *Freshwater Biol.*, **50**, 52–69.

Reynolds, C. S. & Petersen, A. C. 2000. The distribution of planktonic Cyanobacteria in Irish lakes in relation to their trophic status. *Hydrobiologia*, **424**, 91–99.

Sarvala, J., Helminen, H. & Karjalainen, J. 2000. Restoration of Finnish lakes using fish removed: changes in the chlorophyll–phosphorus relationship indicate multiple controlling mechanisms. *Verh. Internat. Verein. Limnol.*, **27**, 1473–1479.

Stutzman, P. 1995. Food quality of gelatinous colonial chlorophytes to the freshwater zooplankters *Daphnia pulicaria* and *Diaptomus oregonensis*. *Freshwater Biol.*, **34**, 149–153.

Taleb, H., Reyes-Marchant, P. & Lair, N. 1994. Effect of vertebrate predation on the spatio-temporal distribution of cladocerans in a temperate eutrophic lake. *Hydrobiologia*, **294**, 117–128.

Tanner, R., Kangur, K., Spoof, L. & Meriluoto, J. 2005. Hepatotoxic cyanobacterial peptides in Estonian freshwater bodies and inshore marine water. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **54**, 41–52.

Thorstrup, L. & Christoffersen, K. 1999. Accumulation of microcystin in *Daphnia magna* feeding on toxic *Microcystis*. *Arch. Hydrobiol.*, **145**(4), 447–467.

Tikhomirova, L. P. 1974. Feeding of some fish species in L. Pskovsko-Chudskoe. *Izvestiya GosNIORKh*, **83**, 131–135 (in Russian).

Vijverberg, J. & Vos, M. 2006. Predator-released compounds, ambient temperature and competitive exclusion among differently sized *Daphnia* species. *Freshwater Biol.*, **51**, 756–767.

Watanabe, M. F., Park, H. & Nakajima, T. 2000. Composition of *Microcystis* and microcystins in Lake Biwa. *Verh. Internat. Verein. Limnol.*, **27**, 2899–2903.

Wetzel, R. G. & Likens, G. E. 1991. *Limnological Analyses*. Springer Verlag.

Wilk-Wozniak, E. & Ligeza, S. 2003. Phytoplankton–nutrient relationships during the early spring and the late autumn in shallow and polluted reservoir. *Oceanol. Hydrobiol. Stud.*, **32**(1), 75–87.

Viimaste aastate radikaalsed muutused Peipsi järve füto- ning zooplanktonis ja nende võimalikud põhjused

Reet Laugaste, Juta Haberman, Teet Krause ja Jaana Salujõe

Füto- ja zooplanktoni dünaamikat Peipsi järves uuriti vegetatsiooniperioodil aastatel 1997–2005, mil zooplanktoni hulk järves hakkas kahanema. Samal ajal näitasid sinivetikad (tsüanobakterid) selget tõusutendentsi: kuni 90%-ni fütoplanktoni biomassist järve lõunaosas. Oktoobris-novembris 2000 toimus *Aphanizomenon flos-aquae* põhjustatud õitseng ja järgmisel aastal ilmnes järsk langus nii füto- kui zooplanktoni, aga eriti keriloomade biomassis. Kõrge veetemperatuuri ja madala veeseisuga augustis 2002 kaasnes sinivetikate põhjustatud õitsenguga kalade suremine. Järgnevatel aastatel oli zooplanktoni biomass väike: alla 1 g m^{-3}. Järve lõunaosas on augustis-septembris hakanud domineerima potentsiaalselt mürgine sinivetikas *Microcystis viridis*. 2002. aastal leitud arvestatav kogus mikrotsüstiine mõlemas järveosas võib olla zooplanktoni, eriti keriloomade hulga kahanemise üheks põhjuseks. Teine tõenäoline põhjus on planktontoiduliste kalade (eriti 0+ koha) tugev press zooplanktonile uurimisperioodil.