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A COMPARATIVE STUDY OF ZOOPLANKTON IN TWO LARGE LAKES OF ESTONIA

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Abstract. The peculiarities of zooplankton communities in two large Estonian lakes are discussed using a comparative approach. L. Peipsi is a moderately eutrophic, L. Võrtsjärv a strongly eutrophic lake. Zooplankton reflects adequately the different trophic state of the studied lakes. In L. Peipsi both the characteristic species of oligo-mesotrophic and eutrophic waters dominate side by side, whereas in L. Võrtsjärv only species of eutrophic waters prevail. In L. Peipsi the mean weight of zooplankters, zooplankton biomass, and production are larger than those in L. Võrtsjärv. Large-bodied zooplankters dominating in L. Peipsi feed mainly on living algae, and the efficient grazing (algal) wood chain prevails in the ecosystem. The small-bodied zooplankters of L. Võrtsjärv are not able to consume large filamentous algae dominating in the lake; they feed on bacteria and detritus, and the food web is dominated by the low efficiency detrital (microbial) chain. The zooplankton of L. Peipsi is in a considerably better state than that of L. Võrtsjärv and can play its role in energy transformation from algae to fish more efficiently. The fish production of L. Peipsi makes up about 0.4% of its phytoplankton production, the fish production of L. Võrtsjärv, 0.2%. This difference is naturally revealed in different fish catches of the lakes: 25–34 kg ha^{-1} in L. Peipsi and 15–20 kg ha^{-1} in L. Võrtsjärv.

Key words: large shallow eutrophic lakes, structure of zooplankton, abundance, biomass, production, trophic relations.

Abbreviations: N = abundance (number) of total zooplankton, thous. ind. m^{-3}; B = biomass of total zooplankton, g m^{-3}; B_{Pred} = biomass of predatory zooplankton, g m^{-3}; B_{Phyt} = biomass of phytoplankton, g m^{-3}; B_{ZP} = biomass of zooplankton, g m^{-3}; P_{Filt} = production of herbivorous zooplankton, g C m^{-2}; P_{Pred} = production of predatory zooplankton, g C m^{-2}; $P_{Filt+Pred}$ = production of total zooplankton, g C m^{-2}; P_{ZP} = production of zooplankton left over for fish after food uptake by predatory zooplankton, g C m^{-2}; PP = production of phytoplankton, g C m^{-2}; C_{Filt} = food consumption by herbivorous zooplankton, g C m^{-2}; C_{Pred} = food consumption by predatory zooplankton, g C m^{-2}.

INTRODUCTION

Because of its intermediate position between phytoplankton and fishes, zooplankton forms an essential link in the food chain of an aquatic ecosystem. The species composition of zooplankton, its dominant species and groups, mean zooplankter weight, biomass and production characterize the trophic state of a lake. It depends on zooplankton how efficiently primarily synthesized organic matter is utilized in the food chain of the waterbody and how fish are supplied with food. Zooplankton affects phytoplankton as well as fishes, both of which exert in their turn influence on zooplankton. The efficiency of energy transformation in a waterbody and its capability for self-sustenance depend largely on zooplankton.

L. Peipsi and L. Võrtsjärv are waterbodies of great importance for Estonia. The lakes yield 95% of the fresh-water fish catch of Estonia. Although L. Peipsi and L. Võrtsjärv are both large and shallow, and hence easily comparable, they have different trophic levels. The goals of the present paper are (1) to study how the relatively slight difference in the trophic state of a waterbody is reflected in the character of its zooplankton and (2) using a comparative approach, to point out specific features of the zooplankton of the two lakes.

DESCRIPTION OF THE LAKES

Lake Peipsi-Pihkva (3558 km^2) is located in East Estonia, on the border between Estonia and Russia. By its surface area, L. Peipsi-Pihkva occupies the fifth place among the lakes of Europe after L. Ladoga (18 135 km^2), L. Onega (9720 km^2), L. Vänern (5585 km^2), and the Saima lake system (4400 km^2). The catchment area (including the lake itself) covers 47 800 km^2 of the territories of Russia, Estonia, and Latvia. L. Peipsi-Pihkva consists of three parts: the largest and deepest northern part L. Peipsi (L. Peipus in older literature, L. Chudskoe in Russian), the middle strait-like part L. Lämmijärv, and the southern part L. Pihkva (L. Pskovskoe in Russian). The present paper deals only with L. Peipsi. The area of L. Peipsi is 2611 km^2 and its volume is 21.8 km^3. About 1500 km^2 of the whole aquatory of L. Peipsi belongs to Estonia, the rest to Russia. L. Peipsi is a relatively shallow (mean depth 8.3 m, maximum depth 12.9 m), moderately eutrophic waterbody. The mean concentrations of total N, total P, and Chl *a* are 724 mg m^{-3}, 33 mg m^{-3}, and 14.7 mg m^{-3}, respectively. The mean transparency is 2.12 m, pH 8.21, and the concentration of O_2 is 11 mg l^{-1}. In the phytoplankton diatoms, mostly *Melosira* species, are dominating during the whole vegetation period. In summer and autumn the bluegreen algae *Aphanizomenon flos-aquae* and *Gloeotrichia echinulata*, causing water blooms, supplement the list of dominant species (Nõges et al., 1996; Lindpere et al., unpubl.). The time of water turnover is about two years. The lake is characterized by a high water level in spring. Long-term fluctuations of the water level with cycles of different duration are evident. The average amplitude of yearly level fluctuations is 1.15 m. There exist only temporary current patterns, which change with the direction of the wind. The lake is holomictic–dimictic, revealing unstable summer stratification, but is well aerated down to the bottom by waves and currents. The ice cover lasts about five months (December–April). Maximum surface temperatures, averaging 21–22 °C, are usually reached in July. Biological summer (with surface temperatures over 10 °C) lasts on an average 134 days (Jaani, 1996). The main commercial fishes are smelt, perch, ruffe, roach, bream, pike, vendace, and pikeperch. The stock of vendace has decreased in recent years, whereas the amount of pikeperch has increased. Considering annual fish catches (9000–12000 tonnes or 25–34 kg ha^{-1}), L. Peipsi outweighs all large lakes in North Europe (Pihu, 1996).

Lake Võrtsjärv is a large (270 km^2) shallow (mean depth 2.8 m, maximum depth 6.0 m) eutrophic (total N 2000 mg m^{-3}, total P 53 mg m^{-3}, Chl *a* 22 mg m^{-3}) lake situated in Central Estonia. The catchment area (3374 km^2) is used for land cultivation and cattle breeding, with 36% of it being under forest. The complete turnover of water occurs on the average once a year. The water of the lake is alkaline (pH 7.5–8.5) with a great buffering capacity. The shallowness of the lake and resuspension of bottom sediments by waves contribute to the formation of a high seston concentration and high turbidity of water during summer. The mean transparency does not exceed 1 m. The gas regime of the lake is good due to continuous mixing. The water temperature reaches its maximum in July (19.8 °C). The ice cover lasts from November till April, on the average 135 days. In summer homothermy prevails, the lake is of a polymictic mixing type. Filamentous algae (*Aulacoseira* spp. in spring, *Planktolyngbya limnetica* and *Limnothrix redekei* in summer and autumn) dominate all the year round. Algal blooms are a common phenomenon in the lake. At present bream, eel, pikeperch, and pike are the main commercial fishes of L. Võrtsjärv. Planktophagous smelt is not abundant. In the 1950s vendace was a commercial fish but its numbers have greatly decreased due to the eutrophication of the lake. The total catch of fish has usually been about 17 kg ha^{-1} (Haberman et al., 1998).

MATERIAL AND METHODS

The material for the present paper was collected monthly in 1991, 1992, and 1993 in L. Võrtsjärv, and biweekly from May to November and in March in 1985–86 and seasonally (March, May–June, July–August, October) in 1992–95 in L. Peipsi. Samples were taken with a quantitative Juday net of 85 μm mesh from one monitoring station in L. Võrtsjärv and from 15 stations in L. Peipsi (Fig. 1).

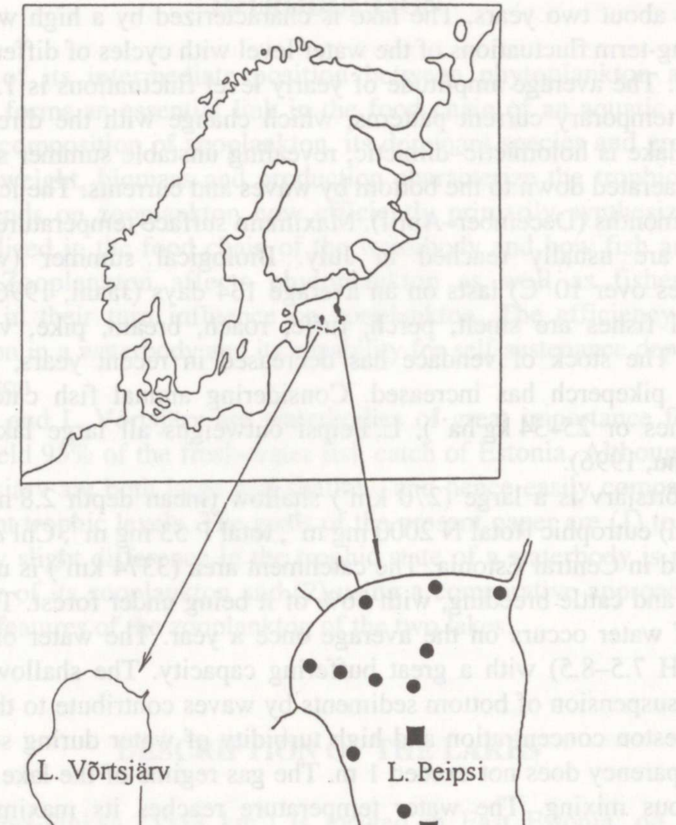

Fig. 1. Location of L. Peipsi and L. Võrtsjärv and the sampling stations.

One-litre samples for analysing rotifers were collected with a Ruttner sampler. The samples were preserved in 4% formaldehyde solution and studied by conventional quantitative analysis (Kiselev, 1956). The individual weights of rotifers were estimated from average lengths according to Ruttner-Kolisko (1977). The lengths of crustaceans were converted to weights according to Studenikina & Cherepakhina (1969, nauplii) and Balushkina & Winberg (1979, other groups). Zooplankton production was calculated applying the physiological method (Winberg, 1971; Waters, 1977; Methodological..., 1984; Ivanova, 1985) making use of the equation

$$P = R\ (k_2 / 1 - k_2),$$

where P is production, R is respiration, and k_2 is the coefficient of growth on assimilated food. For determining R the following equations were employed:

for rotifers $R = 0.106\ W^{0.796}$ (Galkovskaya, 1980),

for cladocerans $R = 0.143\ W^{0.803}$ (Sushchenya, 1972),

for copepods $R = 0.200\ W^{0.777}$ (Sushchenya, 1972),

where W is the average zooplankter weight in grams. The above formulae are valid at $t = 20\ ^\circ$C, in case of different temperatures corrections should be made (Winberg, 1983). The following k_2 values were used: 0.4 for Rotatoria; 0.3 for *Asplanchna*; 0.35 for Cladocera; 0.15 for Copepoda; 0.3 for nauplii. The production of filter-feeders and predators as well as their food consumption were determined separately and are denoted by "Filt" and "Pred" subscript, respectively. Food consumption (uptake, ration) was calculated as

$$C = (P + R) \cdot 1/U,$$

where U is assimilability of food (0.6 for filtrators, 0.8 for predators). The production of zooplankton (P_{ZP}) that is left over for fish was calculated as

$$P_{ZP} = P_{Filt} + P_{Pred} - C_{Pred},$$

where P_{Filt} is the production of herbivorous zooplankton and P_{Pred} the production of predatory zooplankton. The following coefficients were used in zooplankton calculations: 1 mg wet biomass = 0.056 mg C = 0.6 cal = 2.5 J (Ivanova, 1979). For the calculation of zooplankton concentration per square metre, 2.8 and 8.3 m were taken as mean depths in L. Võrtsjärv and in L. Peipsi, respectively.

RESULTS AND DISCUSSION

Dominating species

The species whose numbers and biomass amount to 20% or more of the total zooplankton are considered dominants (Haberman, 1977). In L. Peipsi characteristic species of both eutrophic and oligo-mesotrophic waters dominate side by side. Such coexistence is possible owing to the large size of the lake (with a different trophic state in different parts) and its transition stage from moderately eutrophic (before the early 1960s mesotrophic) to eutrophic. In L. Võrtsjärv only species characteristic of eutrophic waters are dominating (Table 1). All zooplankton species characteristic of oligo-mesotrophic waters

Table 1

Dominating zooplankton species in L. Peipsi and L. Võrtsjärv

Month	L. Peipsi		L. Võrtsjärv	
	N	*B*	*N*	*B*
May	*Polyarthra dolichoptera* *Synchaeta verrucosa* *Keratella cochlearis*	*Bosmina berolinensis* Cyclopoida	*K. cochlearis*	*K. cochlearis* *P. dolichoptera* + *Polyarthra luminosa*
June	*Conochilus unicornis* *K. cochlearis*	*B. berolinensis* Cyclopoida	*P. luminosa* *K. cochlearis*	Cyclopoida (*Mesocyclops* spp.)
July	*Conochilus hippocrepis* *C. unicornis* *Kellicottia longispina* *K. cochlearis* *P. luminosa* *Polyarthra major*	*Daphnia cucullata* *Daphnia galeata* *Eudiaptomus gracilis*	*Anuraeopsis fissa*	*Chydorus sphaericus* *D. cucullata*
August	*C. hippocrepis* *K. cochlearis* *P. luminosa* *P. major*	*D. cucullata* Cyclopoida *P. major*	*A. fissa* *Trichocerca rousseleti*	*Ch. sphaericus*
September	*K. cochlearis* *P. luminosa* *P. major*	*B. berolinensis* *D. galeata* Cyclopoida	*P. luminosa*	*Ch. sphaericus* *P. luminosa*
October	*K. cochlearis* *P. dolichoptera* + *P. luminosa*	*B. berolinensis* *D. galeata* *E. gracilis* Cyclopoida	*K. cochlearis*	*Ch. sphaericus* *Bosmina longirostris*

have totally disappeared or are disappearing (Table 2) from plankton. In strongly eutrophic waterbodies the number of dominating species is small (Andronikova, 1989). In L. Võrtsjärv one to two species, but in L. Peipsi two to four species dominate simultaneously.

Table 2

Changes in the composition of zooplankton in L. Võrtsjärv (1960s to the early 1990s)

Totally disappeared	Nearly disappeared	Abundance has decreased	Abundance has increased
Asplanchna herricki	*Bipalpus hudsoni*	*Asplanchna girodi*	*Anuraeopsis fissa*
Bythotrephes longimanus	*Conochilus unicornis*	*Gastropus stylifer*	*Brachionus angularis*
	Euchlanis lucksiana	*Bosmina c. coregoni*	*B. calyciflorus*
	Kellicottia longispina	*Leptodora kindti*	*Keratella cochlearis*
	Bosmina berolinensis		*K. cochlearis tecta*
	B. obtusirostris		*Pompholyx sulcata*
	Cyclops kolensis		*Trichocerca capucina*
	Eudiaptomus gracilis		*T. rousseleti*
			Bosmina longirostris
			Chydorus sphaericus
			Mesocyclops crassus
			M. leuckarti
			M. oithonoides

Relative importance of different zooplankton groups

The domination of rotifers in a eutrophic waterbody and their increasing share accompanying the eutrophication process are a well-known phenomenon (Reinertsen & Langeland, 1982; Gulati, 1983; Haberman, 1995). The eutrophication process of lakes is accompanied also by an increase in the share of cladocerans and a decrease in the share of copepods (Zánkai & Ponyi, 1986). The proportion of rotifers in the zooplankton of L. Peipsi and L. Võrtsjärv is high since both lakes are eutrophic but in a different stage of eutrophy. As the discrepancy in the trophic levels of the studied lakes is not remarkable, the different share of various zooplankton groups in total zooplankton is not so clearly noticeable as it would be when comparing a eutrophic and an oligotrophic lake. However, the effect of different stages of eutrophy is well revealed when comparing the zooplankton structure of L. Peipsi and L. Võrtsjärv on the basis of the average data of the vegetation period (Fig. 2). The share of rotifers and cladocerans in the plankton of strongly eutrophic L. Võrtsjärv is greater and the share of copepods smaller compared to less eutrophic L. Peipsi.

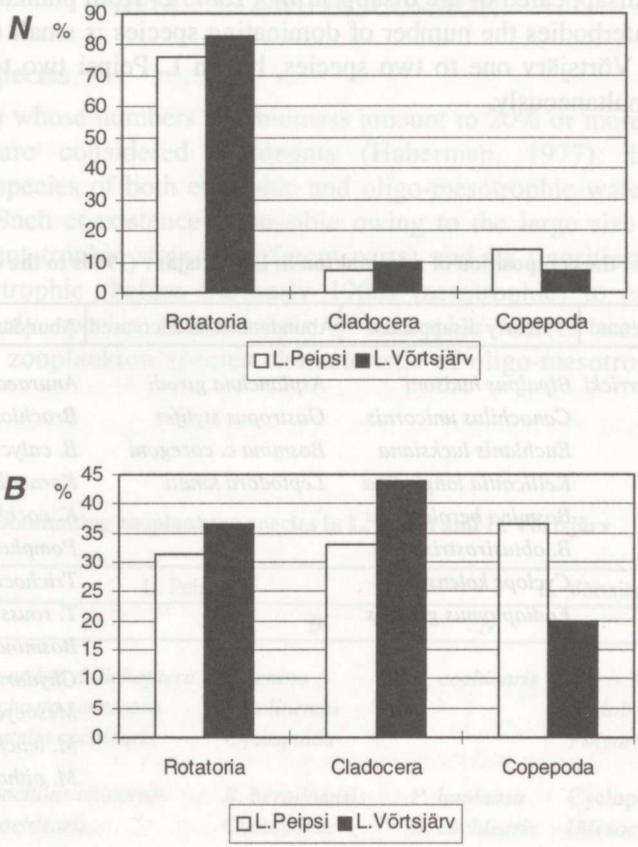

Fig. 2. The share of different zooplankton groups in total zooplankton abundance (*N*) and biomass (*B*) during the vegetation period.

Mean weight of zooplankters

The mean zooplankter weight is quite an informative parameter of the zooplankton community. It characterizes indirectly the trophic relations between phyto- and zooplankton, as well as between zooplankton and fishes; also, it reflects both the pressure of fishes on zooplankton and the lake's trophy. A rise in the trophic level of a waterbody is known to be accompanied by a decrease in the mean zooplankter weight (Gulati, 1990b; Havens, 1994).

In L. Võrtsjärv the mean zooplankter weight fluctuates between 0.4 and 2 µg, average 1.1 µg; in L. Peipsi it fluctuates from 0.8 to 10 µg, average 4 µg (Fig. 3). A zooplankter of moderately eutrophic L. Peipsi is almost 4-fold larger than that of strongly eutrophic L. Võrtsjärv. In L. Võrtsjärv the small mean zooplankter weight is caused by several factors. 1. Small-bodied zooplankters dominate in

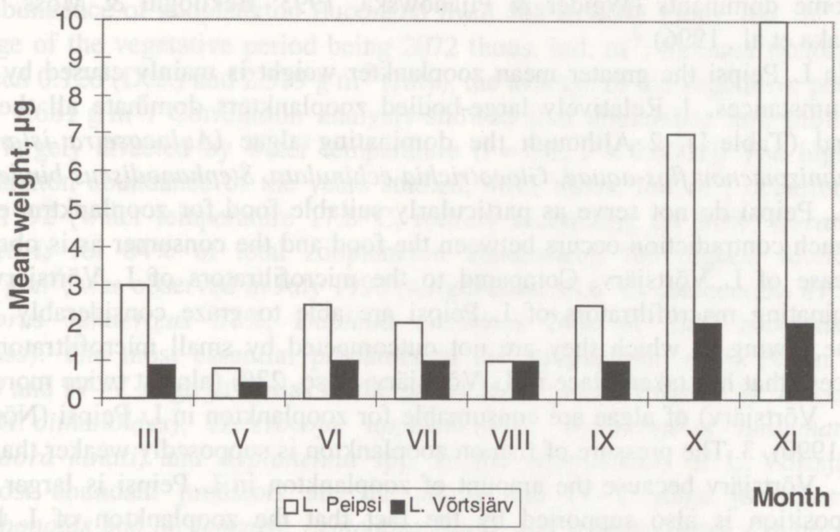

Fig. 3. Mean weights of zooplankters in L. Peipsi and L. Võrtsjärv.

zooplankton all the year round (Table 1). 2. Of large-bodied zooplankters, several species have totally disappeared or are disappearing from plankton (Table 2). 3. Feeding conditions for zooplankton are rather unfavourable. Filamentous algae (*Aulacoseira* spp., *Limnothrix redekei*, *Planktolyngbya limnetica*) dominate in phytoplankton, and only 12% of phytoplankton is consumable for zooplankton (Nõges et al., 1998). Zooplankton is forced to adapt to feeding mainly on bacteria and detritus. Small-bodied microfiltrators are favoured, whereas large-bodied macrofiltrators are disfavoured. Survivors in strongly eutrophic lakes are thus small bacteria feeders. This can be achieved partly by a change in the species composition, partly by changing the proportions of the diet (Pejler, 1983). 4. During the ice-free period the water of shallow L. Võrtsjärv contains a large amount of detritus, 57% of total seston (Nõges & Haberman, 1985). Detritus may inflict considerable harm to filter-feeding zooplankters by clogging up their filter apparatuses and thus inhibiting their feeding and growth. It may also damage their delicate bodies and bring about mass mortality during severe storms. The harmful effect of detritus can account for, at least partly, the modest role and small weight of *Daphnia cucullata* in the summer plankton of L. Võrtsjärv. *D. cucullata* is considerably smaller in L. Võrtsjärv in July (15 µg) than in deeper L. Peipsi (50 µg) where the action of waves does not reach the bottom (Haberman, 1980). 5. The pressure from fish in L. Võrtsjärv can be strong because the amount of zooplankton is relatively small. In case of strong pressure from fish large zooplankters are usually consumed while small ones become dominants (Weider & Pijanowska, 1993; Beklioglu & Moss, 1996; Ohtaka et al., 1996).

In L. Peipsi the greater mean zooplankter weight is mainly caused by three circumstances. 1. Relatively large-bodied zooplankters dominate all the year round (Table 1). 2. Although the dominating algae (*Aulacoseira islandica, Aphanizomenon flos-aquae, Gloeotrichia echinulata, Stephanodiscus binderana*) in L. Peipsi do not serve as particularly suitable food for zooplankton either, no such contradiction occurs between the food and the consumer as is observed in case of L. Võrtsjärv. Compared to the microfiltrators of L. Võrtsjärv, the dominating macrofiltrators of L. Peipsi are able to graze considerably larger algae, owing to which they are not outcompeted by small microfiltrators – a process that has taken place in L. Võrtsjärv. Also, 22% (almost twice more than in L. Võrtsjärv) of algae are consumable for zooplankton in L. Peipsi (Nõges et al., 1990). 3. The pressure of fish on zooplankton is supposedly weaker than it is in L. Võrtsjärv because the amount of zooplankton in L. Peipsi is larger. This supposition is also supported by the fact that the zooplankton of L. Peipsi embodies a large amount of relatively big zooplankters, which would have been eaten up in case of a strong pressure from fish. The occurrence of big plankters is certainly reflected in the mean zooplankter weight.

Number and biomass of zooplankton

L. Peipsi is rich in zooplankton. Its abundance (numbers, *N*) fluctuated between 44 and 2242 thous. ind. m^{-3}, the average of the vegetation period was 1245 thous. ind. m^{-3}; biomass (*B*) ranged from 0.09 to 3.69 g m^{-3}, the average of the vegetation period was 2.305 g m^{-3}. A comparison of large lakes of Europe revealed that the amount of summer zooplankton in L. Onega is about 10-fold smaller than in L. Peipsi, whereas it is 5-fold smaller in L. Ladoga (Smirnova, 1987; Kulikova, 1990). The absolutely highest abundance (4881 thous. ind. m^{-3}), built up mostly of *Conochilus unicornis* and *Keratella cochlearis*, occurred in June 1986 in the central part of the lake pelagial. The highest biomass (17 g m^{-3}) was recorded in July 1992 in the southern part of the lake pelagial where big cladocerans *Daphnia galeata*, *Bosmina berolinensis*, *Bythotrephes longimanus*, and *Leptodora kindti* were simultaneously represented in plankton. However, this biomass is exceptional for L. Peipsi (Haberman, 1996). Both *N* and *B* were in a relatively good correlation with water temperature ($r = 0.5$ and 0.4, respectively; $P < 0.0001$). The influence of water temperature on the zooplankton community is a well-known phenomenon (Beaver & Havens, 1996; Beisner et al., 1996). Herzig (1994) found that abiotic factors (temperature, wind) have the strongest impact on the community in spring and autumn, biotic factors (food, predation) play an important role during summer months.

Zooplankton abundance in L. Võrtsjärv was high, whereas its biomass was low as can be expected in case of a strongly eutrophic lake where the share of small-bodied zooplankters in zooplankton is great and zooplankter weight small.

The abundance of zooplankton fluctuated from 168 to 4048 thous. ind. m^{-3}, the average of the vegetative period being 2072 thous. ind. m^{-3}; biomass fluctuated between 0.126 (Dec.) and 2.579 g m^{-3} (July), the average of the vegetative period being 1.681 g m^{-3}. Correlation analysis showed that abundance and biomass were largely affected by water temperature ($r = 0.7$, $P < 0.0001$). The highest zooplankton abundance of the years studied, 4811 thous. ind. m^{-3}, occurred in May 1992 (water temperature 17.8 °C, rotifers accounting for 96%, *Keratella cochlearis* for 84% of total zooplankton abundance); the highest biomass, 3.541 g m^{-3}, was observed in July 1993 (temperature 18.6 °C, cladocerans 81.3%, *Chydorus sphaericus* 57%, *Daphnia cucullata* 24% of total zooplankton biomass). The most essential predators in the zooplankton of L. Peipsi are adults and IV–V stage juveniles of the genus *Mesocyclops* (mainly *M. leuckarti* and *M. oithonoides*), *Heterocope appendiculata, Bythotrephes longimanus, Leptodora kindti*, and *Asplanchna* spp. In the zooplankton of L. Võrtsjärv, the most abundant predators are the adults and IV–V stage juveniles of *M. oithonoids* and *M. leucarti, Leptodora kindti*, and semipredatory *Asplanchna* spp. like in L. Peipsi. The predatory cladoceran *B. longimanus* disappeared from the plankton of L. Võrtsjärv already in the 1960s, and *H. appendiculata* has never been found in this lake. The share of predatory zooplankton biomass (B_{Pred}) in the total zooplankton biomass fluctuated from 6.8 (June) to 26.8 (July) in L. Peipsi and from 10.6 (Sept.) to 27.5 (June) in L. Võrtsjärv, the average of both lakes being about 18%.

The abundance of zooplankton in L. Võrtsjärv is almost 2-fold higher and biomass 1.5-fold lower than in L. Peipsi (Fig. 4). The causes of this discrepancy are the difference in the dominating zooplankters in these lakes (Table 1) as well as the consequent difference in the mean zooplankter weight (Fig. 3). The higher the trophic level, the greater is the discrepancy between zooplankton abundance and biomass. High abundance can be accompanied by very low biomass.

Production of zooplankton

In L. Peipsi P_{Filt} fluctuated between 0.05 and 5.9 g C m^{-2} $month^{-1}$; P_{Pred} between 0.002 and 0.69 g C m^{-2}; the production of the whole zooplankton community ($P_{Filt+Pred}$) ranged from 0.06 in March to 6.3 g C m^{-2} in August. During the period between May and October herbivores produced 20.6, predators 1.8, and the whole zooplankton community 22.4 g C m^{-2} (Haberman, 1996).

In L. Võrtsjärv the zooplankton production was low as expected because life conditions for zooplankton are poor in this lake. P_{Filt} fluctuated between 0.03 and 1.6 g C m^{-2} $month^{-1}$; P_{Pred} between 0 and 0.2 g C m^{-2}; $P_{Filt+Pred}$ ranged from 0.03 in December to 1.7 g C m^{-2} in July. During the period between May and October herbivores produced 5.5, predators 0.5, and the whole zooplankton community 6 g C m^{-2}. In L. Peipsi the production of zooplankton is almost 4-fold higher than in L. Võrtsjärv (Fig. 5). The production of predatory zooplankton made up about 7% of the total zooplankton production ($P_{Pred}/P_{Filt+Pred} = 0.065$) in L. Peipsi and

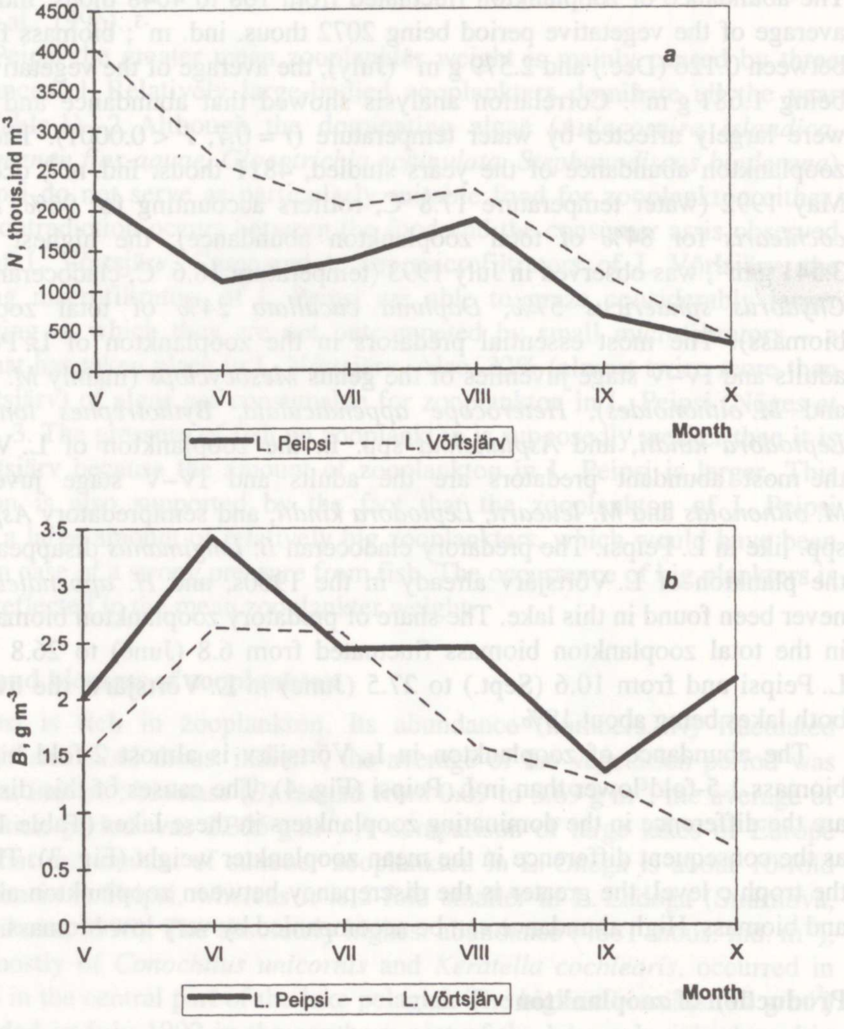

Fig. 4. The dynamics of zooplankton abundance (*a*) and biomass (*b*) in L. Peipsi and L. Võrtsjärv during the vegetation period.

8% ($P_{Pred}/P_{Filt+Pred}$ = 0.08) in L. Võrtsjärv. In June, when the adults and IV–V stage juveniles of the genus *Mesocyclops* are numerous in L. Võrtsjärv, the share of predatory zooplankton in plankton is the greatest (13%). In L. Peipsi it is the greatest in July (9%), when large predatory cladocerans *B. longimanus* and *L. kindti* are abundant.

In L. Peipsi the production of the whole zooplankton community per vegetation period was 22.4 g C m^{-2}. Of this the amount reaching fish (P_{ZP})

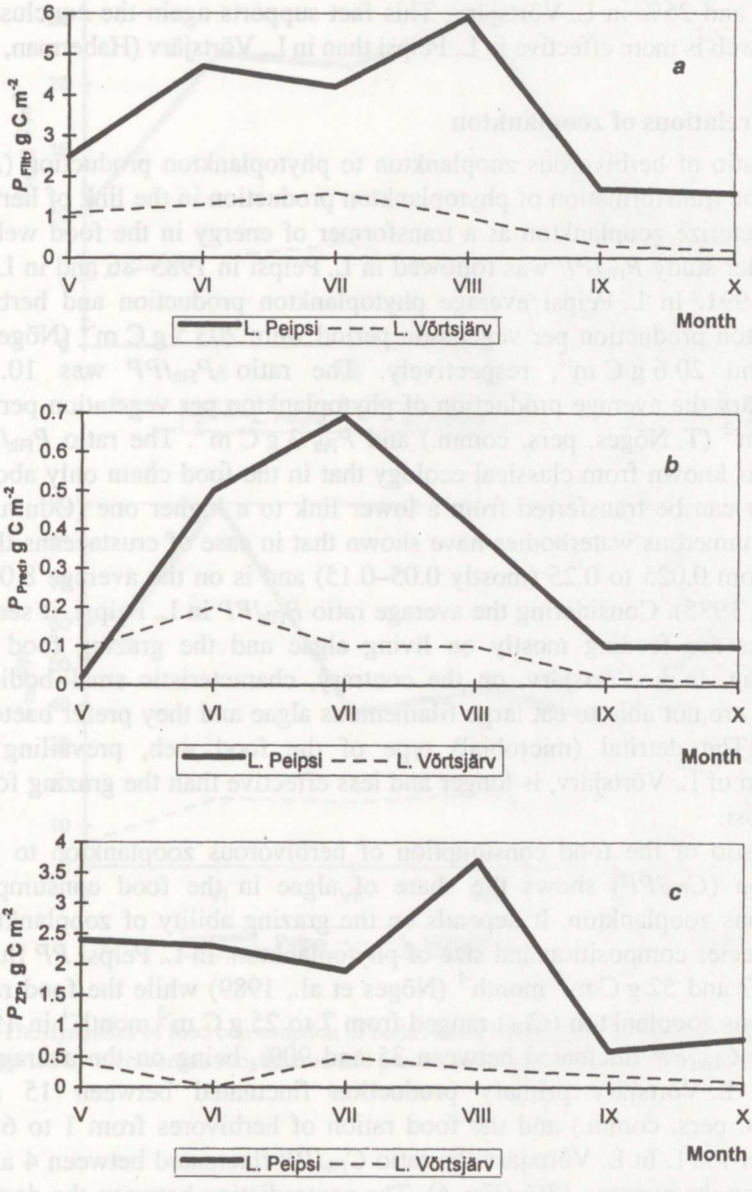

Fig. 5. The dynamics of zooplankton production in L. Peipsi and L. Võrtsjärv during vegetation period. *a*, herbivorous zooplankton; *b*, predatory zooplankton; *c*, zooplankton left over for fish.

was 11.7 g C m^{-2}. In L. Võrtsjärv $P_{Filt+Pred}$ and P_{ZP} were 6 and 1.5 g C m^{-2}, respectively. This means that about 50% of the zooplankton reached fish in L. Peipsi and 25% in L. Võrtsjärv. This fact supports again the conclusion that the food web is more effective in L. Peipsi than in L. Võrtsjärv (Haberman, 1996).

Trophic relations of zooplankton

The ratio of herbivorous zooplankton to phytoplankton production (P_{Filt}/PP) reflects the transformation of phytoplankton production in the link of herbivores. To characterize zooplankton as a transformer of energy in the food web of the lakes under study P_{Filt}/PP was followed in L. Peipsi in 1985–86 and in L. Võrtsjärv in 1991. In L. Peipsi average phytoplankton production and herbivorous zooplankton production per vegetation period were 203.5 g C m^{-2} (Nõges et al., 1993) and 20.6 g C m^{-2}, respectively. The ratio P_{Filt}/PP was 10.1%. In L. Võrtsjärv the average production of phytoplankton per vegetation period was 130 g C m^{-2} (T. Nõges, pers. comm.) and P_{Filt} 3 g C m^{-2}. The ratio P_{Filt}/PP was 2.3%. It is known from classical ecology that in the food chain only about 10% of energy can be transferred from a lower link to a higher one (Odum, 1959). Data on numerous waterbodies have shown that in case of crustaceans this ratio ranges from 0.025 to 0.25 (mostly 0.05–0.15) and is on the average $8.0 \pm 1.1\%$ (Ivanova, 1985). Considering the average ratio P_{Filt}/PP in L. Peipsi, it seems that herbivores are feeding mostly on living algae and the grazing food web is dominating. In L. Võrtsjärv, on the contrary, characteristic small-bodied zooplankters are not able to eat large filamentous algae and they prefer bacteria and detritus. The detrital (microbial) type of the food web, prevailing in the ecosystem of L. Võrtsjärv, is longer and less effective than the grazing food web of L. Peipsi.

The ratio of the food consumption of herbivorous zooplankton to primary production (C_{Filt}/PP) shows the share of algae in the food consumption of herbivorous zooplankton. It depends on the grazing ability of zooplankters and on the species composition and size of phytoplankton. In L. Peipsi PP fluctuated between 7 and 52 g C m^{-2} month^{-1} (Nõges et al., 1989) while the food ration of herbivorous zooplankton (C_{Filt}) ranged from 7 to 25 g C m^{-2} month^{-1} in 1985–86. The ratio C_{Filt}/PP fluctuated between 35 and 90%, being on the average about 50%. In L. Võrtsjärv primary production fluctuated between 15 and 38 (T. Nõges, pers. comm.) and the food ration of herbivores from 1 to 6 g C m^{-2} month^{-1} in 1991. In L. Võrtsjärv the ratio C_{Filt}/PP fluctuated between 4 and 18% and was on the average 12% (Fig. 6). The contradiction between the dominating species of phyto- and zooplankton, related to the trophic state, is reflected also by the ratio C_{Filt}/PP. In L. Peipsi it is about 4-fold higher than in L. Võrtsjärv. The data on the dominating zooplankters in L. Peipsi and L. Võrtsjärv (Table 1) and their mean weights (Fig. 3) provide ground to expect that zooplankton consumes more algae in L. Peipsi than in L. Võrtsjärv. The grazing efficiency of zooplankton depends largely on the weight of grazers. It has been established that

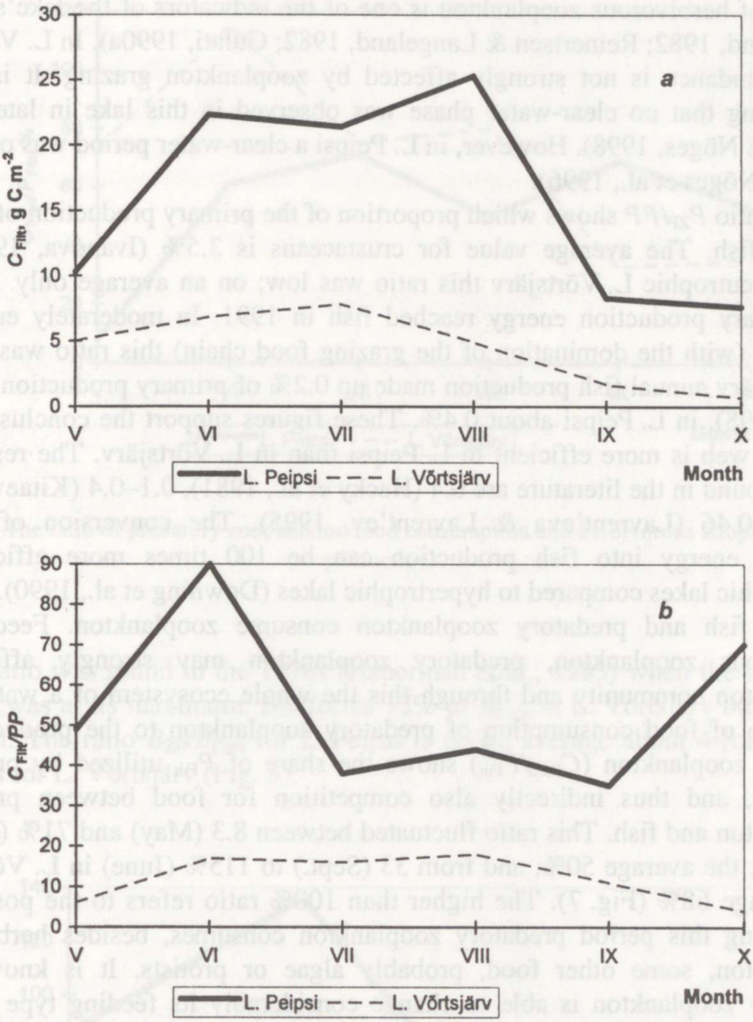

Fig. 6. The dynamics of food consumption of herbivorous zooplankton (*a*) and the ratio of food consumption by herbivorous zooplankton and production of phytoplankton (*b*) in L. Peipsi and L. Võrtsjärv.

large zooplankters have a higher grazing efficiency than smaller ones (Salonen & Arvola, 1988). Of all crustaceans, large daphnids have the highest grazing capacity (Pace & Vaque, 1994; Jürgens & Stolpe, 1995). In the lakes under study, correlation analysis revealed also a positive relationship between the mean zooplankton weight and grazing (L. Peipsi: $r = 0.5$; L. Võrtsjärv: $r = 0.4$, $P < 0.0001$). In lakes of high trophy the role of zooplankton in controlling algal abundance is usually less pronounced than in oligo-mesotrophic lakes. The grazing of herbivorous zooplankton is one of the indicators of the lake's trophy (Langeland, 1982; Reinertsen & Langeland, 1982; Gulati, 1990a). In L. Võrtsjärv algal abundance is not strongly affected by zooplankton grazing. It is worth mentioning that no clear-water phase was observed in this lake in late spring (Nõges & Nõges, 1998). However, in L. Peipsi a clear-water period was observed in June (Nõges et al., 1996).

The ratio P_{ZP}/PP shows which proportion of the primary production of energy reaches fish. The average value for crustaceans is 3.5% (Ivanova, 1985). In strongly eutrophic L. Võrtsjärv this ratio was low; on an average only 1.1% of the primary production energy reached fish in 1991. In moderately eutrophic L. Peipsi (with the domination of the grazing food chain) this ratio was 6%. In L. Võrtsjärv annual fish production made up 0.2% of primary production (Nõges et al., 1998), in L. Peipsi about 0.4%. These figures support the conclusion that the food web is more efficient in L. Peipsi than in L. Võrtsjärv. The respective figures found in the literature are 0.4 (Hecky et al., 1981), 0.1–0.4 (Kitaev, 1984) or 0.02–0.46 (Lavrent'eva & Lavrent'ev, 1995). The conversion of phytoplankton energy into fish production can be 100 times more efficient in oligotrophic lakes compared to hypertrophic lakes (Downing et al., 1990).

Both fish and predatory zooplankton consume zooplankton. Feeding on herbivorous zooplankton, predatory zooplankton may strongly affect the zooplankton community and through this the whole ecosystem of a waterbody. The ratio of food consumption of predatory zooplankton to the production of filtrative zooplankton (C_{Pred}/P_{Filt}) shows the share of P_{Filt} utilized by predatory plankters, and thus indirectly also competition for food between predatory zooplankton and fish. This ratio fluctuated between 8.3 (May) and 71% (July) in L. Peipsi, the average 50%; and from 33 (Sept.) to 115% (June) in L. Võrtsjärv, the average 68% (Fig. 7). The higher than 100% ratio refers to the possibility that during this period predatory zooplankton consumes, besides herbivorous zooplankton, some other food, probably algae or protists. It is known that predatory zooplankton is able to change considerably its feeding type (Arndt, 1993; Santer, 1993; Branstrator, 1995). Since P_{Filt} is rather low in L. Võrtsjärv, predatory zooplankton can be a real food competitor for fish during certain periods (especially in June). In L. Peipsi predatory zooplankton is not a serious food competitor for fish.

To characterize the trophic state of a waterbody the ratio of zooplankton to phytoplankton biomass (B_{ZP}/B_{Phyt}) has been often used. This ratio decreases with the rise of the trophic level of a waterbody (Gulati, 1983; Rognerud & Kjellberg, 1984; Zánkai & Ponyi, 1986; a.o.). In oligotrophic waterbodies it is $\geq 4:1$, in mesotrophic $1:1$, in eutrophic $\leq 1:2$ (Andronikova, 1989). In L. Peipsi the ratio ranges between 0.02 and 1.54, being on an average 0.5 per year and 0.7 between May and October. In strongly eutrophic L. Võrtsjärv the ratio ranges between 0.06 and 0.22 during the vegetation period, with an average of 0.13, which refers to the rather high trophic level of L. Võrtsjärv. The lowest average value (0.04)

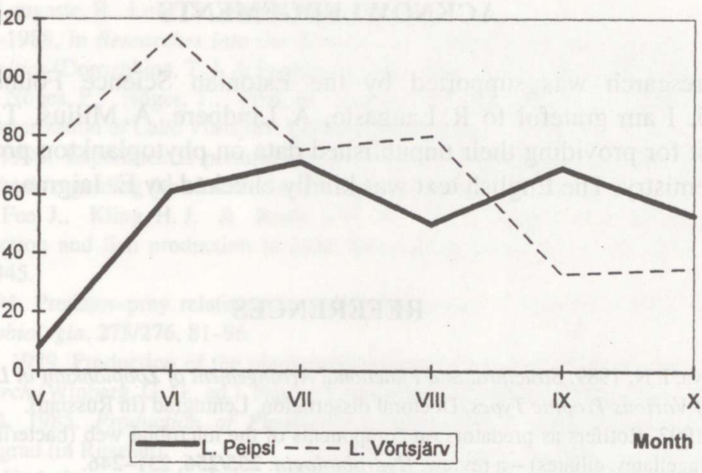

Fig. 7. The ratio of predatory zooplankton food consumption and herbivorous zooplankton production.

of this ratio was found in the 1970s (Haberman et al., 1983) when the trophy of the lake was at its maximum. B_{ZP} forms 13% of B_{Phyt} in L. Võrtsjärv but 50% in L. Peipsi. The ratio B_{ZP}/B_{Phyt} for L. Peipsi is on an average about 4-fold higher than it is for L. Võrtsjärv (Fig. 8).

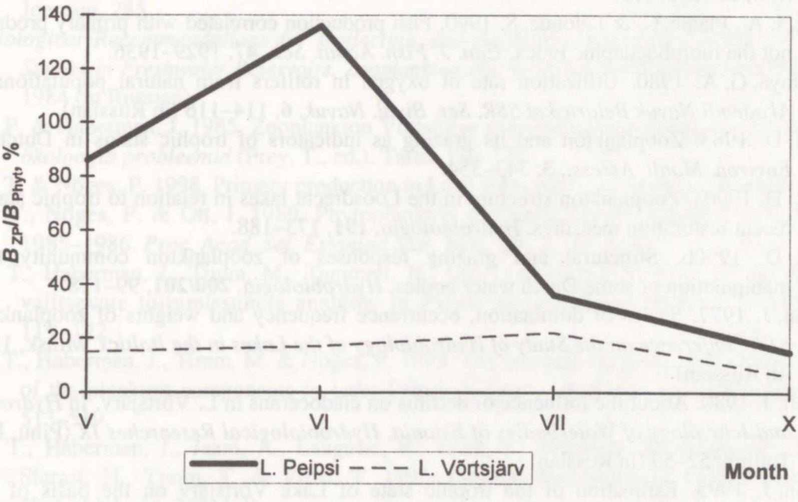

Fig. 8. The ratio of zooplankton biomass and phytoplankton biomass in L. Peipsi and L. Võrtsjärv.

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REFERENCES

Andronikova, I. N. 1989. *Structural and Functional Arrangement of Zooplankton in Lake Ecosystems of Various Trophic Types*. Doctoral dissertation. Leningrad (in Russian).

Arndt, H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. *Hydrobiologia*, **255/256**, 231–246.

Balushkina, E. V. & Winberg, G. G. 1979. Relationship between the body mass and length of planktonic animals. In *Headlines of Water Ecosystem Research* (Winberg, G. G., ed.). Nauka, Leningrad, 169–172 (in Russian).

Beaver, J. R. & Havens, K. E. 1996. Seasonal and spatial variation in zooplankton community structure and their relation to possible controlling variables in Lake Okeechobee. *Freshwat. Biol.*, **36**, 45–56.

Beisner, B. E., McCauley, E. & Wronas, F. 1996. Temperature-mediated dynamics of planktonic food chains: The effect of an invertebrate carnivore. *Freshwat. Biol.*, **35**, 219–232.

Beklioglu, M. & Moss, B. 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. *Freshwat. Biol.*, **36**, 315–325.

Branstrator, D. K. 1995. Ecological interactions between *Bythotrephes cederstroemi* and *Leptodora kindtii* and the implications for species replacement in Lake Michigan. *J. Great Lakes Res.*, **21**, 670–679.

Downing, J. A., Plante, C. & Lalonde, S. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aquat. Sci.*, **47**, 1929–1936.

Galkovskaya, G. A. 1980. Utilization rate of oxygen in rotifers from natural populations. *Vesti Akademii Navuk Belaruskai SSR, Ser. Biyal. Navuk*, **6**, 114–116 (in Russian).

Gulati, R. D. 1983. Zooplankton and its grazing as indicators of trophic status in Dutch lakes. *Environ. Monit. Assess.*, **3**, 343–354.

Gulati, R. D. 1990a. Zooplankton structure in the Loosdrecht lakes in relation to trophic status and recent restoration measures. *Hydrobiologia*, **191**, 173–188.

Gulati, R. D. 1990b. Structural and grazing responses of zooplankton community to biomanipulation of some Dutch water bodies. *Hydrobiologia*, **200/201**, 99–118.

Haberman, J. 1977. Scales of domination, occurrence frequency and weights of zooplankters. In *XIX Conference on the Study of Hydrobiology of the Lakes in the Baltics*. Minsk, 153–154 (in Russian).

Haberman, J. 1980. About the influence of detritus on cladocerans in L. Võrtsjärv. In *Hydrobiology and Ichtyology of Waterbodies of Estonia. Hydrobiological Researches IX* (Pihu, E., ed.). Tallinn, 52–59 (in Russian).

Haberman, J. 1995. Estimation of the trophic state of Lake Võrtsjärv on the basis of rotifers (Rotatoria). *Proc. Estonian Acad. Sci. Biol.*, **44**, 3/4, 92–105.

Haberman, J. 1996. Contemporary state of zooplankton in Lake Peipsi. *Hydrobiologia*, **338**, 113–123.

Haberman, J., Laugaste, R., Lokk, S., Nõges, P. & Tammert, H. 1983. Plankton of L. Võrtsjärv in 1964–1988. In *Researches into the Biology and Fishery Management of Waterbodies in the Baltics* (Dorozhkina, T. J. & Perminov, L. G., eds.). Pskov, 60–63 (in Russian).

Haberman, J., Nõges, P., Nõges, T., Pihu, E., Kangur, K., Kangur, A. & Kisand, V. 1998. Characterization of Lake Võrtsjärv. *Limnologica*, in press.

Havens, K. E. 1994. Experimental perturbation of a freshwater plankton community: A test of hypothesis regarding the effects of stress. *Oikos*, **69**,147–153.

Hecky, R. E., Fee, J., Kling, H. J. & Rudd, J. W. M. 1981. Relationship between primary production and fish production in Lake Tanganyika. *Trans. American Fish. Soc.*, **110**, 336–345.

Herzig, A. 1994. Predator–prey relationships within the pelagic community of Neusiedler See. *Hydrobiologia*, **275/276**, 81–96.

Ivanova, M. B. 1979. Production of the planktonic crustaceans. In *Headlines of Water Ecosystem Research* (Winberg, G. G., ed.). Nauka, Leningrad, 155–169 (in Russian).

Ivanova, M. B. 1985. *Production of Planktonic Crustaceans in Fresh Waters*. Lenuprizdat, Leningrad (in Russian).

Jaani, A. 1996. Hydrology and water balance of Lake Peipsi. *Hydrobiologia*, **338**, 11–23.

Jürgens, K. & Stolpe, G. 1995. Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake. *Freshwat. Biol.*, **33**, 27–38.

Kiselev, J. A. 1956. Methods of plankton research. In *Freshwater Biota of the USSR IV* (Pavlovski, E. N. & Zhadin, V. I., eds.). Izd. Akad. Nauk, Moscow, 183–265 (in Russian).

Kitaev, S. P. 1984. *Ecological Fundamentals of Bioproductivity in Lakes of Different Geographical Zones*. Nauka, Moscow (in Russian).

Kulikova, T. P. 1990. Zooplankton. In *Ecosystem of L. Onega* (Kaufman, Z. S., ed.). Nauka, Leningrad, 207–216 (in Russian).

Langeland, A. 1982. Interaction between zooplankton and fish in a fertilized lake. *Holarct. Ecol.*, **5**, 273–310.

Lavrent'eva, G. M. & Lavrent'ev, P. J. 1995. The relationship between fish yield and primary production in large European freshwater lakes. In *Abstracts of the First International Lake Ladoga Symposium 1993* (Simola, H., Viljanen, M., Slepuhina, T. & Murthy, R., eds.). Joensuu, 285.

Methodological Recommendations for Collecting and Analysing Materials for Hydrobiological Studies in Freshwater Reservoirs. Zooplankton and Its Production. Lenuprizdat, Leningrad, 1984 (in Russian).

Nõges, P. & Haberman, J. 1985. Zooplankton Võrtsjärve esmastoodangu kasutajana. In *Kaasaegse ökoloogia probleemid* (Frey, T., ed.). Tartu, 180–182.

Nõges, T. & Nõges, P. 1998. Primary production in Lake Võrtsjärv. *Limnologica*, in press.

Nõges, T., Nõges, P. & Ott, I. 1989. Phytoplankton production in the pelagial of L. Peipsi in 1985–1986. *Proc. Acad. Sci. Estonian SSR. Biol.*, **38**, 2, 123–130.

Nõges, T., Haberman, J., Timm, M., Tammert, H., Ott, I. & Nõges, P. 1990. Peipsi planktonis valitsevate toitumissuhete analüüs. In *Peipsi järve seisund* (Timm, T., ed.). Tartu, 119–122.

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

Nõges, T., Haberman, J., Jaani, A., Laugaste, R., Lokk, S., Mäemets, A., Nõges, P., Pihu, E., Starast, H., Timm, T. & Virro, T. 1996. General description of Lake Peipsi-Pihkva. *Hydrobiologia*, **338**, 1–9.

Nõges, T., Nõges, P., Haberman, J., Kisand, V., Kangur, K., Kangur, A. & Järvalt, A. 1998. Food web structure in shallow eutrophic Lake Võrtsjärv (Estonia). *Limnologica*, in press.

Odum, E. P. 1959. *Fundamentals of Ecology*. W. B. Saunders Co, Philadelphia.

Ohtaka, A., Mori, N & Saito, S. 1996. Zooplankton composition in the Tsugaru-Juniko Lakes, Northern Japan, with reference to predation impact. *Jpn. J. Limnol.*, **57**, 1, 15–26.

Pace, M. L. & Vaque, D. 1994. The importance of *Daphnia* in determining mortality rates of protozoans and rotifers in lakes. *Limnol. Oceanogr.*, **39**, 985–996.

Pejler, B. 1983. Zooplanktic indicators of trophy and their food. *Hydrobiologia*, **101**, 111–114.

Pihu, E. 1996. Fishes, their biology and fisheries management in Lake Peipsi. *Hydrobiologia*, **338**, 163–172.

Reinertsen, H. & Langeland, A. 1982. The effect of a lake fertilization on the stability and material utilization of a limnetic ecosystem. *Holarct. Ecol.*, **5**, 311–324.

Rognerud, S. & Kjellberg, G. 1984. Relationships between phytoplankon and zooplankton biomass in large lakes. *Verh. Int. Ver. Limnol.*, **22**, 666–671.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of planktonic rotifers. *Arch. Hydrobiol.*, **8**, 71–76.

Salonen, K. & Arvola, L. 1988. A radiotracer study of zooplankton grazing in two small humic lakes. *Verh. Int. Ver. Limnol.*, **23**, 462–469.

Santer, B. 1993. Potential importance of algae in the diet of adult *Cyclops vicinus*. *Freshwat. Biol.*, **30**, 269–278.

Smirnova, T. S. 1987. Zooplankton. In *Contemporary State of Ecosystem in L. Ladoga* (Petrova, N. A. & Raspletina, G. F., eds.). Nauka, Leningrad, 119–126.

Studenikina, E. I. & Cherepakhina, M. M. 1969. Mean weight of dominant zooplankters in the Azov Sea. *Gidrobiol. zhurnal*, **5**, 89–91 (in Russian).

Sushchenya, L. M. 1972. *Respiration Intensity of Crustaceans*. Naukova dumka, Kiev (in Russian).

Zánkai, N. P. & Ponyi, J. E. 1986. Composition, density and feeding of crustacean zooplankton community in a shallow, temperate lake (Lake Balaton, Hungary). *Hydrobiologia*, **135**, 131–147.

Waters, T. F. 1977. Secondary production in Inland Waters. *Adv. Ecol. Res.*, **10**, 91–164.

Weider, L. J. & Pijanowska, J. 1993. Particity of *Daphnia* life histories in response to chemical cues from predators. *Oikos*, **67**, 385–392.

Winberg, G. G. (ed.). 1971. *Method for Estimation of Production of Aquatic Animals*. Academic Press, New York.

Winberg, G. G. 1983. Vant-Hoff's temperature coefficient and Arrhenius' equation in biology. *Obshchaya biol.*, **44**, 1, 31–42 (in Russian).

KAHE EESTI SUURJÄRVE ZOOPLANKTONI VÕRDLEV ANALÜÜS

Juta HABERMAN

Peipsi järv on mõõdukalt eutroofne, kuid Võrtsjärv tugevalt eutroofne järv. Erinev troofsus peegeldub selgesti nende järvede zooplanktoni koosluse iseloomus. Peipsi järve zooplanktonis esinevad kõrvuti oligo-mesotroofsete ning eutroofsete vete liigid, Võrtsjärves ainult eutroofsed liigid. Peipsi järve zooplankter on keskmiselt neli korda, zooplanktoni biomass poolteist korda ning produktsioon peaaegu neli korda suurem kui Võrtsjärves. Peipsis domineerivad suured zooplankterid toituvad põhiliselt elusatest vetikatest ning järve ökosüsteemi toiduahelas toimib efektiivne vetikaringe. Võrtsjärve väikesed zooplankterid ei suuda süüa järves valdavaid suuri niitvetikaid, nad toituvad bakteritest ja detriidist ning toiduahelas on ülekaalus väheefektiivne mikroobidetriidiringe. Peipsi järves on zooplankton tunduvalt paremas seisundis kui Võrtsjärves ning suudab tõhusamalt täita oma osa energia transformeerimisel vetikatest kaladeni. Peipsi järves moodustab kalaproduktsioon umbes 0,4%, Võrtsjärves aga 0,2% fütoplanktoni produktsioonist. Loomulikult kajastub see ka järvede kalasaagis: Peipsi järves 25–34 kg ha^{-1}, Võrtsjärves 15–20 kg ha^{-1}.