Proc. Estonian Acad. Sci. Biol. Ecol., 2000, **49**, 1, 34–51
https://doi.org/10.3176/biol.ecol.2000.1.03

DOMINANT ZOOPLANKTON SPECIES IN LAKE PEIPSI

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Received 8 June 1999, in revised form 30 September 1999

Abstract. Lake Peipsi or Lake Peipsi–Pihkva (Pskovsko-Chudskoe ozero in Russian) is a large (3555 km^2) shallow (mean depth 7.1 m) moderately eutrophic waterbody with total nitrogen and phosphorus contcentrations respectively 768 and 42 mg m^{-3}. Planktivorous smelt dominates in the fish fauna. The species of zooplankton whose abundance and biomass amount to 20% or more of total zooplankton are considered dominants. In L. Peipsi both characteristic species of oligo-mesotrophic (*Conochilus hippocrepis*, *C. unicornis*, *Kellicottia longispina*, *Bosmina berolinensis*) and eutrophic waters (*Keratella cochlearis*, *Daphnia cucullata*, *Bosmina c. coregoni*, sometimes even *Anuraeopsis fissa* and *Keratella tecta*) are among the dominants. Rotifer species dominate with respect to number throughout the year, while cladocerans and copepods dominate with respect to biomass. Species of the genera *Bosmina* and *Daphnia* and the copepod *Eudiaptomus gracilis* play very important roles in plankton in summer and autumn. The dominant species have not changed during more than 30 years (since 1965), but the degree of dominance (%) has changed. The percentage of oligotrophic species has decreased, whereas eutrophic species have become more abundant.

Key words: zooplankton, dominant species, moderately eutrophic lake, Lake Peipsi.

INTRODUCTION

Increasing trophy brings about profound changes in the plankton of a waterbody. In phytoplankton, filamentous and colony-forming algae whose size makes them unsuitable as food for zooplankton (*Planktolyngbya limnetica* (Lehman & Sandgren), *Limnothrix redekei* (Van Goor) Meffert, *Aphanothece saxicola* Näg., *Microcystis aeruginosa* Kütz., *Aulacoseira* spp.) will become dominant. Larger, phytoplankton-feeding zooplankters – macrofiltrators – will disappear from the plankton community due to poor feeding conditions. Predominance in zooplankton will be gained by microfiltrators – rotifers and small cladocerans (*Chydorus sphaericus* (O. F. Müller), *Bosmina longirostris* (O. F. Müller)) – for

whom bacteria and detritus serve as the most suitable food items. In the food web of the ecosystem an ineffective microbial loop (phytoplankton → bacteria + detritus → zooplankton → fish) starts to prevail. This will result also in reduced fish production.

The described process has not yet taken place in moderately eutrophic L. Peipsi. In the lake which is one of the richest in fish among European lakes, the dominant fish is plankton-feeding smelt (*Osmerus e. eperlanus* m. *spirinchus* Pallas). Being consumed not only by planktivorous fishes but also by the fry of all fish species, zooplankton determine largely the fish production of the lake. In the food web of L. Peipsi the effective food chain (phytoplankton → zooplankton → fish) is dominating, which means that the zooplankton of the lake are feeding largely on living algae (Nõges et al., 1993). Consequently, the lake must provide a sufficient amount of zooplankters–macrofiltrators and small algae edible for zooplankton. Large smelt catches indicate that planktivorous fishes do not generally suffer for food deficit. Since the 1930s the annual smelt catch in the lake has been mostly 1500–3500 t with a maximum of 9160 t in 1935 (Pihu, 1996). According to Odum (1959), about 10–20% of the energy is transferred from each link of the food web to the next one, while 80–90% of the energy is dispersed. The shorter the food web, the more efficient it is, i.e. the larger proportion of the solar energy assimilated by phytoplankton reaches fish. In moderately eutrophic L. Peipsi, 6% of the phytoplankton energy reaches fish (Haberman, 1996), while in strongly eutrophic L. Võrtsjärv the respective figure is 3% (Haberman, 1998). Considering that fish catch forms generally about 25–35% of the fish production (Bul'on & Winberg, 1981), the production of fish in L. Peipsi ranges from 0.83 to 1.4 g C m^{-2}, i.e. forms 0.4–0.7% of the primary production. The relevant indicator on other lakes by the literature is 0.1–0.4% (Kitaev, 1984) or 0.02–0.46% (Lavrent'eva & Lavrent'ev, 1995). This demonstrates also that the transformation of solar energy to fish production is efficient in L. Peipsi.

The present paper gives a survey of dominant zooplankters in the zooplankton community of L. Peipsi as efficient transformers of energy, able to effectively transform the energy of phytoplankton to fish production.

MATERIAL AND METHODS

The material discussed in the present paper was collected in 1965–67, 1971, 1978, 1979, 1981, 1985–87, and 1992–99. Samples were taken with a quantitative Juday net of 85 μm mesh from the lake pelagial in 1965–81, from the central part of the lake pelagial in 1985–87, and from the whole pelagial of the Estonian part of the lake in 1992–99. In the last two years (1998, 1999) rotifers were gathered with a bathometer. Altogether about 2000 zooplankton samples were analysed. The samples were preserved in 4% formaldehyde solution and studied by

conventional quantitative methods (Kiselev, 1956). Individual rotifer masses were estimated from average lengths according to Ruttner-Kolisko (1977). Lengths of crustaceans were converted into masses according to Studenikina & Cherepakhina (1969) and Balushkina & Winberg (1979). As the use of plankton nets leads to underestimation of rotifers, correction coefficients were employed. These coefficients, calculated by comparing simultaneous net and bathometer samples, increase rotifer numbers 1 to 27 times (Virro, 1989).

DESCRIPTION OF THE LAKE

Lake Peipsi (3555 km^2) is located in East Estonia, on the border between Estonia and Russia. It consists of three parts: the largest and deepest northern part L. Peipsi *s.s.* (2611 km^2), the middle strait-like part L. Lämmijärv (Teploe ozero in Russian; 236 km^2), and the southern part L. Pihkva (Pskovskoe ozero; 708 km^2). Of the 3555 km^2 surface area, 1570 km^2 belongs to Estonia, the rest to Russia. Lake Peipsi is a relatively shallow (mean depth 7.1 m), moderately eutrophic waterbody. The mean concentrations of total N, total P, and Chl *a* are 768, 42, and 14.7 mg m^{-3}, respectively. The mean transparency is 1.9 m, pH 8.28, and the concentration of O_2 is 10 mg L^{-1}. The retention time is about two years. Water level fluctuations are considerable, with an amplitude of 3.04 m. The ice cover lasts about five months (December–April). Biological summer (with surface water temperatures over 10 °C) lasts on an average 134 days (Jaani, 1996). Maximum surface water temperatures, averaging 21–22 °C, are usually reached in July. Diatoms and blue-green algae prevail with respect to biomass, diatoms and green algae, with respect to the number of phytoplankton cells. The average biomass of phytoplankton fluctuates in the range 1–16 g m^{-3} in spring, 3–125 g m^{-3} in summer, and 5–35 g m^{-3} in autumn (Haberman et al., 2000). The total count of bacteria fluctuates between 2.2×10^6 and 4.3×10^6 cells mL^{-1} and the average number of saprophytic bacteria ranges from 98 to 360 cells mL^{-1} (Lokk & Kisand, 1996). Lake Peipsi is one of the richest in fish among European lakes. The total annual catch of fish is usually 25–31 kg ha^{-1}. As planktivorous smelt dominates in the fish fauna, zooplankton are a very important component of this ecosystem (Pihu, 1996). The number of zooplankton fluctuates between 46 thous. and 2752 thous. ind m^{-3}, with an average of 974 thous. ind m^{-3}; wet biomass ranges from 0.09 to 6.344 g m^{-3}, with a summer average of 3.092 g m^{-3}.

RESULTS AND DISCUSSION

A zooplankton community is best characterized by its dominant species. Domination implies successful reproduction and development, which befalls only to the species for whom conditions in the waterbody are suitable. Dominant

species characterize indirectly but quite adequately the whole waterbody and its ecosystem. They reflect the waterbody's trophic level, type of the food web, amount and composition of algae as food for zooplankton, supply of fish with food, quality of fish food, and the degree of pressure exerted by fish on zooplankton.

The zooplankton taxa that make up 20% or more of the total zooplankton number and biomass are considered dominants (Haberman, 1977). Along with the character species of oligo-mesotrophic waters (*Conochilus hippocrepis* (Schrank), *C. unicornis* (Rousselet), *Kellicottia longispina* (Kellicott), *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 even *Anuraeopsis fissa* (Gosse) and *Keratella tecta* (Gosse)) (Table 1). 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

Table 1. Dominant zooplankton species in L. Peipsi

Month	Number	Biomass
March	*Polyarthra dolichoptera* Idelson, *Synchaeta verrucosa* Nipkow, *Keratella cochlearis* (Gosse)	*Eudiaptomus gracilis* (Sars), Cyclopoida
May	*P. dolichoptera*, *S. verrucosa*, *K. cochlearis*, *Keratella quadrata* (Müller)	*Bosmina berolinensis* Imhof, Cyclopoida
June	*Conochilus unicornis* (Rousselet), *K. cochlearis*, *Kellicottia longispina* (Kellicott), *K. quadrata*, *P. dolichoptera*	*B. berolinensis*, Cyclopoida, *Daphnia galeata* Sars, *Daphnia cristata* Sars, *Daphnia cucullata* Sars
July	*C. unicornis*, *Conochilus hippocrepis* (Schrank), *K. longispina*, *K. cochlearis*, *Polyarthra luminosa* (Kutikova), *Polyarthra major* (Burckhardt), *Anuraeopsis fissa* (Gosse), *Keratella tecta* (Gosse)	*D. galeata*, *D. cucullata*, *D. cristata*, *Diaphanosoma brachyurum* (Liéven), *Limnosida frontosa* Sars, *Leptodora kindti* (Focke), *Bythotrephes longimanus* Leydig, *E. gracilis*, Cyclopoida
August	*C. hippocrepis*, *P. luminosa*, *P. major*, *K. cochlearis*, *A. fissa*, *K. tecta*	*D. cucullata*, Cyclopoida
September	*K. cochlearis*, *P. luminosa*, *P. major*	*B. berolinensis*, *Bosmina c. coregoni* Baird, *Bosmina gibbera* Schoedler, *D. galeata*, Cyclopoida
October	*K. cochlearis*, *P. luminosa*, *P. dolichoptera*	*B. berolinensis*, *Bosmina c. coregoni*, *B. gibbera*, *D. galeata*, *E. gracilis*, Cyclopoida
November	*P. dolichoptera*, *S. verrucosa*, *K. cochlearis*	*B. berolinensis*, *E. gracilis*

moderately eutrophic (before the early 1960s mesotrophic) to eutrophic. The species dominating with respect to number and those dominating with respect to biomass are presented separately. The former reflect quite adequately the living conditions (water temperature, food, oxygen regime, pH, trophy, etc.) in a water-body. The latter give evidence, above all, of the content of organic matter in zoo-plankton, zooplankton as an energy transformer, and zooplankton as food for fish. With respect to number, small rotifers are dominant throughout the year, while with respect to biomass, considerably larger cladocerans and copepods prevail.

Dominant species with respect to number

Synchaeta verrucosa Nipkow is present in L. Peipsi, depending on water temperature, from late October or early November up to late May or early June (Fig. 1). Its development is most intensive in May at water temperatures of 3–6 °C. In the other large lake of Estonia, Võrtsjärv, which is shallow and warms more rapidly, intensive development of *S. verrucosa* takes place earlier, in April (Haberman, 1995). *S. verrucosa* starts to disappear when the water temperature rises above 10 °C, but a few individuals can be met at temperatures as high as 14 °C. Males and resting eggs have been found just before and at the time of the population maximum (Virro & Haberman, 1993). In L. Peipsi the number of *S. verrucosa* ranges from 1000 to 460 000 ind. m^{-3}, with biomass from 0.001 to 0.628 g m^{-3}, averages being 20 000 ind. m^{-3} and 0.020 g m^{-3}. In the warm-water period, the thermophobic *S. verrucosa* is replaced by eurythermal species of the genus (*S. kitina* Rousselet, *S. oblonga* Ehrenberg, *S. pectinata* Ehrenberg, *S. stylata* Wierzejski), but the latter are never particularly abundant.

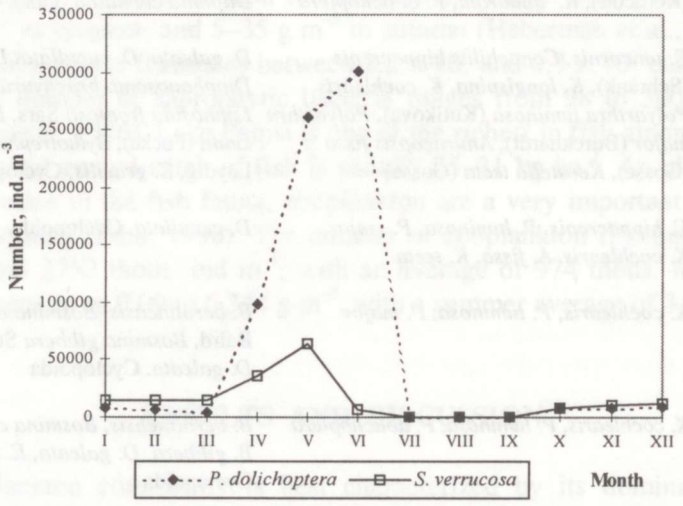

Fig. 1. Number of *Synchaeta verrucosa* and *Polyarthra dolichoptera*.

Polyarthra dolichoptera Idelson (Fig. 1) is found at almost the same temperatures as *S. verrucosa*. It appears in October when the water temperature falls to 9–10 °C and its development comes to an end in June, soon after the period of sexual reproduction. The number of *P. dolichoptera* in L. Peipsi fluctuates in the range of 2733–858 600 ind. m^{-3} and the biomass 0.001–0.429 g m^{-3}. The mean number for the whole period the species occurs is 78 200 ind. m^{-3} and the mean biomass 0.039 g m^{-3}. In summer *P. dolichoptera* is replaced by several congeneric species: *P. longiremis* Carlin, *P. luminosa* Kutikova, *P. major* Burckhardt, and *P. remata* Skorikov. However, only *P. luminosa* and *P. major* attain dominance in the summer plankton.

Polyarthra luminosa and ***P. major*** appear in June at water temperatures of about 12–13 °C. Both species become dominants already in July and reach their maximum abundance in August (Fig. 2). From then on, their numbers start to decrease, and both species disappear from the plankton, depending on water temperature, in late October or early November. The population density of *P. luminosa* ranges from 3400 to 677 000 ind. m^{-3} and its biomass from 0.002 to 0.406 g m^{-3} with averages of 72 500 ind. m^{-3} and 0.036 g m^{-3}. The respective figures for *P. major* are: 2000–988 000 ind. m^{-3}, 0.002–0.790 g m^{-3}, with averages of 125 548 ind. m^{-3} and 0.1 g m^{-3}.

Keratella cochlearis (Gosse) is represented in the plankton of L. Peipsi practically all the year round (Fig. 3) with several seasonally alternating morpho-ecological forms: *hispida*, *macracantha*, *nordica*, *pustulata*, *robusta*, *tecta*, and *typica*. *Keratella cochlearis* f. *macracantha* and f. *nordica* are associated with colder periods, whereas f. *tecta* and f. *pustulata* occur in warmer periods (Eloranta, 1982; Virro & Haberman, 1993). Recently *K. c. hispida* and *K. c. tecta*

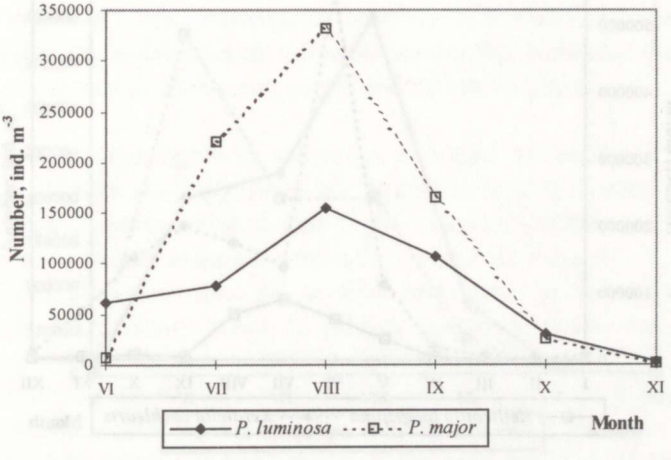

Fig. 2. Number of *Polyarthra luminosa* and *P. major*.

began to be treated as independent species – *K. hispida* (Lauterborn) and *K. tecta* (Gosse). *Keratella cochlearis* has always been a dominant species in L. Peipsi but its abundance increased notably in the 1980s when the trophic level of the lake was the highest of the recent period (Möls et al., 1996). In the 1960s *K. tecta* occurred in L. Peipsi only as single individuals but in the 1980s several cases of dominance of this species were reported in the more eutrophic southern parts of the lake (L. Lämmijärv, Värska Bay in L. Pihkva). Its average number (from July to October) in southern parts of the lake is 34 000 ind. m^{-3} and biomass 0.003 g m^{-3}. Numerous researchers have established a relationship between an increase in the population density of *K. tecta* and a rise of the trophic level (De Manuel & Armengol, 1993; Fussman, 1993; Karabin & Ejsmont-Karabin, 1993; etc.). Although *K. cochlearis* is a rotifer with a wide ecological range it is always more abundant in eutrophic waters. In strongly eutrophic L. Võrtsjärv it has numbered higher than 2×10^6 ind. m^{-3} in May (Haberman, 1995) and in moderately eutrophic L. Peipsi almost 1×10^6 ind. m^{-3} in June. Pejler (1962) found a strong correlation between the trophic level and the spine length of *K. cochlearis* in Swedish lakes in summer. Only long-spined individuals occurred in oligotrophic lakes, while forms with short spines or without spines dominated in eutrophic lakes. The eutrophic indicator *K. tecta* lacks a spine. In L. Peipsi *K. cochlearis* occurs at water temperatures of 0–23.8 °C, the optimal temperature being about 18 °C. This last fact is confirmed also by the existence of abundance maxima at roughly this water temperature (Fig. 3). In L. Peipsi the population density of *K. cochlearis* varies in the range of 2700–900 000 ind. m^{-3} (average 121 000 ind. m^{-3}) and biomass 0.0005–0.18 g m^{-3} (0.024 g m^{-3}).

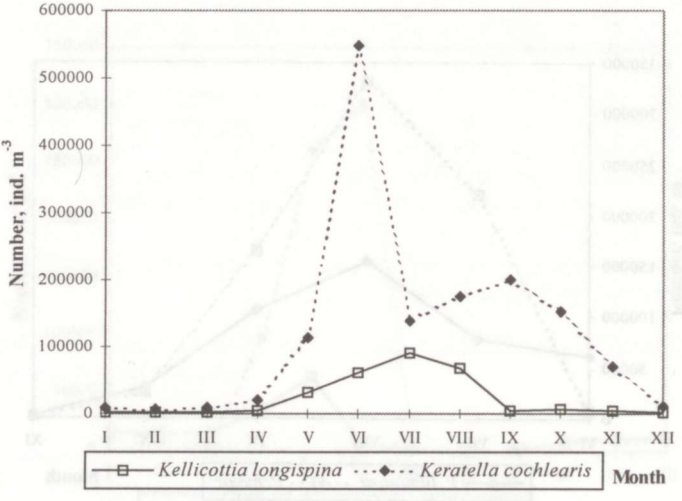

Fig. 3. Number of *Keratella cochlearis* and *Kellicottia longispina*.

Although ***Keratella quadrata*** (Müller) does not belong to the main dominants, it may occasionally become a dominant species. It is present throughout the year, but its number and biomass are the highest in June (202 000 ind. m^{-3}, 0.138 g m^{-3}). The average number in L. Peipsi is 60 500 ind. m^{-3} and biomass 0.042 g m^{-3}.

Kellicottia longispina (Kellicott) has also dominated quite frequently in the zooplankton of L. Peipsi with respect to abundance. It is a species of oligo-mesotrophic waters (Kutikova, 1970; Hofmann & Höfle, 1993), whose abundant occurrence reflects a moderate trophic level of the lake. In strongly eutrophic L. Võrtsjärv this species is rare (Haberman, 1998). The number of *K. longispina* in L. Peipsi varies from 761 to 633 000 ind. m^{-3}, biomass from 0.0002 to 0.133 g m^{-3}, with mean values of 23 361 ind. m^{-3} and 0.007 g m^{-3}, respectively. The seasonal dynamics of the population density of the species is shown in Fig. 3.

Conochilus unicornis (Rousselet) is a species with a broad ecological range, which can live in small numbers even in strongly eutrophic waters (Kutikova & Haberman, 1986), but clearly prefers less trophic water (Pejler, 1965; Kutikova, 1970). It has always been abundant in the zooplankton of L. Peipsi (Haberman, 1976b; Mäemets, 1966). Although *K. cochlearis* and *C. unicornis* are regarded as competitors for food (Pejler, 1957), the ample food supply of the lake allows their successful coexistence. Mass occurrence of *C. unicornis* in L. Peipsi is an evidence of the relatively good state of the lake. It appears in L. Peipsi at water temperatures of 8–9 °C and has its maximum abundance at about 17 °C. This species is found in small numbers even in October and as single individuals, all the year round. *C. unicornis* occurs in plankton together with ***Conochilus hippocrepis*** (Schrank), a species with similar ecological requirements (Fig. 4). Evidently, these species are competitors for food but their temperature

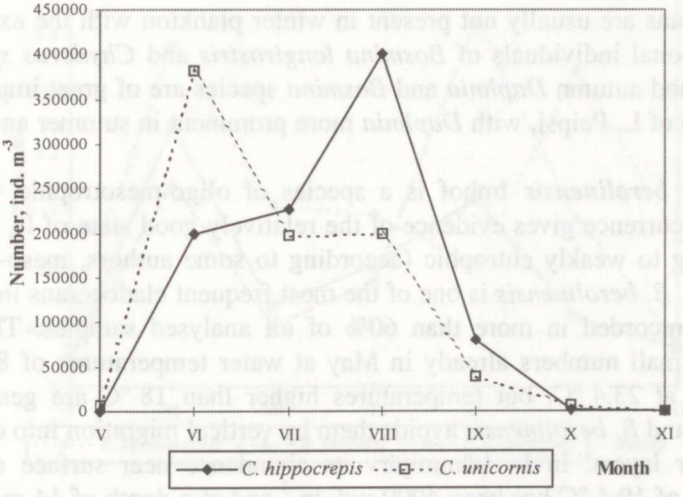

Fig. 4. Number of *Conochilus hippocrepis* and *C. unicornis*.

preferences are slightly different, because whenever one of them is abundant, the other is represented in relatively modest numbers. *C. hippocrepis* appears to prefer higher temperatures than *C. unicornis*. Individuals of *C. unicornis* have sometimes been found in May and even in early November, but this is usually not the case with *C. hippocrepis*. The abundance of *C. unicornis* in L. Peipsi fluctuates between 394 000 and 853 000 ind. m^{-3}, biomass between 0.197 and 0.426 g m^{-3}; the mean values are 119 000 ind. m^{-3} and 0.059 g m^{-3}. The respective figures for *C. hippocrepis* are 254 000–982 000 ind. m^{-3} and 0.127–0.491 g m^{-3}; 130 000 ind. m^{-3} and 0.065 g m^{-3}. *C. unicornis* is more abundant in early summer, whereas *C. hippocrepis* is more numerous in late summer (Virro & Haberman, 1993).

Anuraeopsis fissa (Gosse) is a well-known indicator of eutrophy (Gulati, 1990; Langley et al., 1995). In the 1960s it occurred only in the most eutrophic part of L. Peipsi *s.l.* – L. Pihkva – but was not found in L. Peipsi *s.s.* However, in the 1980s *A. fissa* was occasionally a dominant in the southern part of L. Peipsi *s.s.*, while in midsummer its domination was common in Värska Bay in L. Pihkva. In the 1990s it has been among dominants on several occasions in the southern part of L. Peipsi *s.s.* and more frequently in L. Lämmijärv. Increasing population density of *A. fissa* is a sign of danger attributed to transition to a higher trophic level. In L. Peipsi the number of *A. fissa* fluctuates in the range of 11 700–169 200 ind. m^{-3}, biomass 0.0001–0.001 g m^{-3}. Being a thermophilous plankter it is most abundant in July–August when it can be a dominant in zooplankton abundance.

Dominant species with respect to biomass

Cladocerans are usually not present in winter plankton with the exception of some occasional individuals of *Bosmina longirostris* and *Chydorus sphaericus*. In summer and autumn *Daphnia* and *Bosmina* species are of great importance in the plankton of L. Peipsi, with *Daphnia* more prominent in summer and *Bosmina* in autumn.

Bosmina berolinensis Imhof is a species of oligo-mesotrophic waters. Its abundant occurrence gives evidence of the relatively good state of L. Peipsi and its belonging to weakly eutrophic (according to some authors, meso-eutrophic) waterbodies. *B. berolinensis* is one of the most frequent cladocerans in L. Peipsi, which was recorded in more than 60% of all analysed samples. The species appears in small numbers already in May at water temperatures of 8–10 °C. It occurs also at 23.4 °C, but temperatures higher than 18 °C are generally not favourable, and *B. berolinensis* avoids them by vertical migration into deeper and cooler water layers. In L. Lämmijärv its abundance near surface at a water temperature of 19.4 °C has been 4000 ind. m^{-3} and at a depth of 14 m and water temperature of 15.2 °C, 16 000 ind. m^{-3} (Haberman, 1976a). *B. berolinensis*

occurs abundantly still in October–November at a water temperature of about 7 °C. It has been found even at water temperatures of 2–8 °C; however, it disappears when the water temperature falls further. Moderate thermophility of the species is revealed by two peaks in its seasonal development – in June and October (Fig. 5). The number of *B. berolinensis* fluctuates between 254 and 66 552 ind. m^{-3}, and its biomass is 0.002–1.978 g m^{-3}, the mean numbers of the vegetation period (May–October) being 6189 ind. m^{-3} and 0.171 g m^{-3}.

Bosmina c. coregoni Baird is a character species of eutrophic waters. In the 1960s, *B. c. coregoni* was never a dominant in L. Peipsi *s.s.*; however, it frequently was in more trophic L. Lämmijärv and very frequently in most trophic L. Pihkva. In the 1980s, with increasing trophic level (Möls et al., 1996), several occasions of domination of *B. c. coregoni* were recorded also in the southern part of L. Peipsi *s.s.* In the 1990s, when further increase in trophy must have stopped as a result of falling agricultural pollution, an opposite trend could be expected. However, occasional episodes of dominance of *B. c. coregoni* have still been observed in L. Peipsi. During the current research this species was found at water temperatures of 0.1–23.4 °C. The number of *B. c. coregoni* in the plankton becomes noteworthy in spring at water temperatures of 8–10 °C, but the optimum water temperature for this cladoceran is about 18 °C. Higher temperatures start to inhibit its reproduction. In autumn, at water temperatures of 5–7 °C, *B. c. coregoni* can still be abundant. Although the species is seldom a dominant, it occurs in considerable numbers from May to November. Its average monthly numbers have fluctuated in the range of 282–50 760 ind. m^{-3} (average value of the occurrence period 5478 ind. m^{-3}) and biomass 0.005–0.863 g m^{-3} (0.096 g m^{-3}).

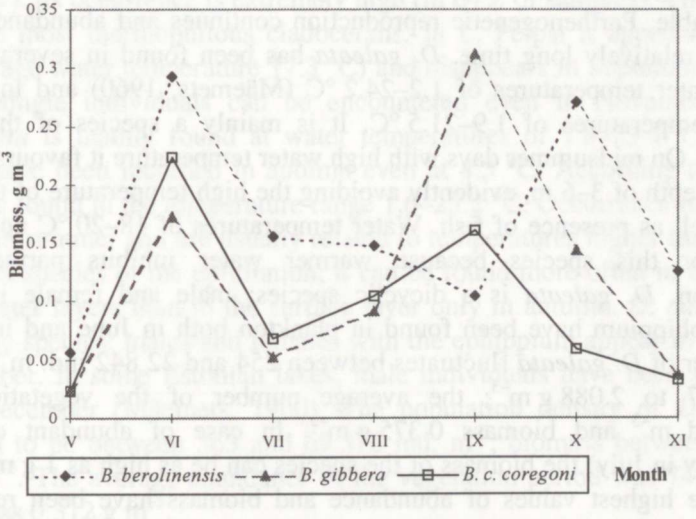

Fig. 5. Biomass of *Bosmina berolinensis*, *B. c. coregoni*, and *B. gibbera*.

The numbers of *B. c. coregoni* and *B. berolinensis* are quite similar, but since individuals of *B. c. coregoni* are smaller than those of *B. berolinensis*, their biomasses are different (Fig. 5). The biomass of *B. c. coregoni* is the largest in September. The average wet biomass of a female *B. c. coregoni* in L. Peipsi is 0.02 mg.

Bosmina gibbera Schoedler is a zooplankter of meso-eutrophic waters. It is rare in Estonian lakes but occurs frequently in L. Peipsi. Sometimes, especially in autumn, the species is a dominant in the total zooplankton biomass. It appears in spring at a temperature of about 10 °C and disappears in autumn at 4.5–5 °C. The author has encountered the species in L. Peipsi at water temperatures of 4.5–21.8 °C. Like all species of the genus *Bosmina*, *B. gibbera* is not particularly thermophilous and it occurs in large numbers in June and September–October (Fig. 5). The range of its number in L. Peipsi is 1658–19 642 ind. m^{-3} and of biomass 0.024–0.312 g m^{-3}, with the respective mean values of 7050 ind. m^3 and 0.115 g m^{-3}. The length of an individual may vary from 0.41 to 0.50 mm, the average wet biomass being 0.017 mg.

Daphnia galeata Sars tends to be a species of oligo-mesotrophic waters and it does not thrive in eutrophic waters. For instance, in the second largest Estonian lake, strongly eutrophic L. Võrtsjärv, it is totally lacking (Haberman, 1998). In L. Peipsi this cladoceran is frequent and has been found in more than 50% of samples. Since *D. galeata* is a large zooplankter (0.03–0.08 mg), its percentage in the zooplankton biomass is often large. It appears in the plankton in late May or early June (at water temperatures above 10 °C) and remains there up to October–November (Fig. 6). In autumn, it has still been abundant at water temperatures of 4–5 °C. As in L. Peipsi the phytoplankton biomass is large in October (Laugaste et al., 1996), the feeding conditions for algivorous *D. galeata* are favourable. Parthenogenetic reproduction continues and abundance remains high for a relatively long time. *D. galeata* has been found in several Estonian lakes at water temperatures of 1.2–24.2 °C (Mäemets, 1960) and in L. Peipsi at water temperatures of 1.9–21.5 °C. It is mainly a species of the pelagial epilimnion. On midsummer days with high water temperature it favours the water layer at a depth of 3–6 m, evidently avoiding the high temperature of the surface layer as well as presence of fish. Water temperatures of 18–20 °C appear to be optimal for this species because warmer water inhibits parthenogenetic reproduction. *D. galeata* is a dicyclic species; male and female individuals with the ephippium have been found in plankton both in June and in October. The number of *D. galeata* fluctuates between 254 and 22 842 ind. m^{-3}, biomass from 0.007 to 2.088 g m^{-3}; the average number of the vegetation period is 5574 ind. m^{-3} and biomass 0.375 g m^{-3}. In case of abundant occurrence (particularly in July) the biomass of the species can be as high as 1 g m^{-3} or even higher. The highest values of abundance and biomass have been recorded in July (Fig. 6), while some increase in October is also characteristic of the species. It has been noted that *D. galeata* reaches sexual maturity at a relatively small

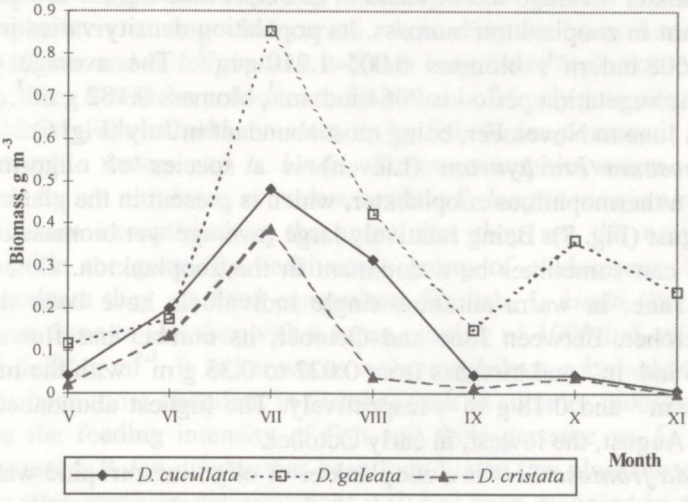

Fig. 6. Biomass of *Daphnia galeata*, *D. cucullata*, and *D. cristata*.

weight in L. Peipsi. In the presence of invertebrate predators that feed selectively on small zooplankton, fast-growing individuals with a large size must be favoured at the first reproduction, while fish predation, affecting large individuals, must favour small size at the first reproduction (Lampert, 1993).

Daphnia cucullata Sars is a species of eutrophic waters. Its high abundance in L. Peipsi reminds one of the fact that the lake is after all eutrophic (although moderately). Its occurrence is extremely high (in 64% of samples). The species is one of the most thermophilous cladocerans. In L. Peipsi it appears usually in June (average water temperature 17.3 °C) and disappears in September–October, although single individuals can be encountered even in November (Fig. 6). *D. cucullata* is mainly found at water temperatures of 7.8–23.4 °C but small numbers have been recorded in autumn even at 4.5 °C. According to Mäemets (1960) it is found in the temperature range 1.6–25.2 °C. Occurrence maxima take place in midsummer and are usually related to temperatures higher than 20 °C. It is a distinct species of the epilimnion; it can be found more often in near-bottom warmer water layers than in the surface layer only in autumn. *D. cucullata* is a monocyclic species; males and females with the ephippium appear in most cases in September. In some Estonian lakes, male individuals have been found from July to December (Mäemets, 1960). The population density of *D. cucullata* was found to be between 363 and 69 372 ind. m^{-3}, biomass between 0.01 and 2.992 g m^{-3}. The average abundance of the vegetation period was 7452 ind. m^{-3} and biomass 0.312 g m^{-3}.

Daphnia cristata Sars is a species of oligo-mesotrophic waters. Compared with *D. cucullata* and *D. galeata* it occurs rarely. However, since it is a relatively

large zooplankter (average wet biomass in L. Peipsi 0.03 mg), it can occasionally be a dominant in zooplankton biomass. Its population density varies in the range of 363–40 608 ind. m^{-3}, biomass 0.005–1.210 g m^{-3}. The average population density of the vegetation period is 7064 ind. m^{-3}, biomass 0.182 g m^{-3}. *D. cristata* occurs from June to November, being most abundant in July (Fig. 6).

Diaphanosoma brachyurum (Liéven) is a species of oligo-mesotrophic waters. It is a thermophilous zooplankter, which is present in the plankton mainly in July–August (Fig. 7). Being relatively large (average wet biomass in L. Peipsi 0.05 mg) it can sometimes be a dominant in the zooplankton. *D. brachyurum* appears in June; in warm autumns single individuals have been met as late as early October. Between June and October, its number has fluctuated from 564 to 6566 ind. m^{-3} and biomass from 0.022 to 0.33 g m^{-3} with the mean values of 4139 ind. m^{-3} and 0.18 g m^{-3}, respectively. The highest abundance has been recorded in August, the lowest, in early October.

Limnosida frontosa Sars is a zooplankter of oligo-mesotrophic waters. It is a thermophilous species, being most abundant in the warmest months of summer, July–August, and disappearing from plankton already in September (Fig. 7). Because of its rare occurrence but large size (0.1 mg), *L. frontosa* has occasionally accounted for 20% or more of the zooplankton biomass. Its population density varies in the range 564–7614 ind. m^{-3}, biomass in the range 0.056–1.528 g m^{-3}; the mean number being 2202 ind. m^{-3} and mean biomass 0.33 g m^{-3}. Because *L. frontosa* is a character species of less trophic, i.e. cleaner waters, its low occurrence is an unfavourable parameter for the lake. On the other hand, one has to keep in mind that fish consume this species eagerly.

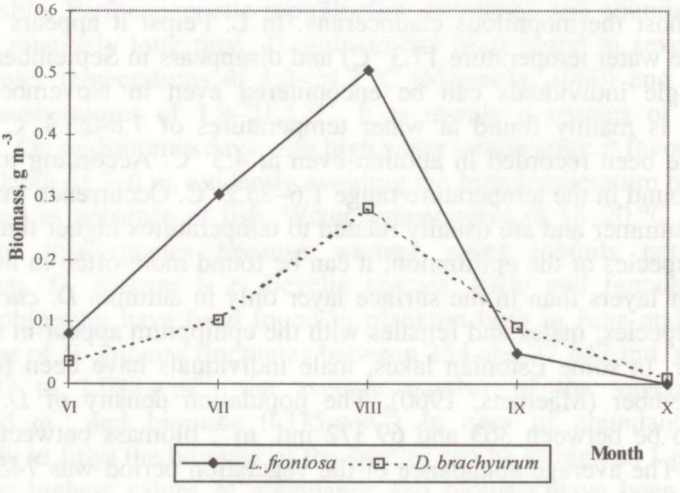

Fig. 7. Biomass of *Diaphanosoma brachyurum* and *Limnosida frontosa*.

Bythotrephes longimanus Leydig and ***Leptodora kindti*** (Focke) are the largest zooplankters among cladocerans. According to Manuilova (1964) *L. kindti* is 2–10 mm and *B. longimanus* 2–5 mm long. Once a plankter of such size occurs in a lake, it will be a dominant in biomass. Mostly juvenile forms were present: evidently, adults had been eaten up by fish. *B. longimanus* is a species of oligo-mesotrophic waters and *L. kindti* of meso-eutrophic waters. *L. kindti* is characterized by not numerous occurrence, while *B. longimanus* is a rare species. Both species are exceptional in the sense that they are the only predatory plankters within the generally herbivorous group of cladocerans. Feeding on other zooplankters they are food competitors for fish. *L. kindti* (juv.) occurs in plankton from June to October with a mean number of 1096 ind. m^{-3} and mean biomass of 0.296 g m^{-3}. It is known as a thermophilous zooplankter, but in L. Peipsi it has been more abundant in October than in summer months. Evidently, at that time the feeding intensity of fish and their pressure on *L. kindti* have already decreased. *B. longimanus* has been found in so few plankton samples that it is hard to state anything definite about it. It has been recorded in August with the population density of 677 ind. m^{-3} and biomass of 0.338 g m^{-3}. Preferring lower trophy, *B. longimanus* disappeared from L. Võrtsjärv already in the 1960s (Haberman, 1998). Its very rare occurrence in L. Peipsi indicates that this lake is not a suitable habitat for this species any more.

Among copepods, only juvenile forms of Cyclopoida and adult forms of *Eudiaptomus gracilis* are dominants in L. Peipsi.

Eudiaptomus gracilis (Sars) is a eurythermic copepod, which occurs in plankton throughout the year (Fig. 8). It has been found at water temperatures of 0.1–23.4 °C. The most suitable temperature for its development seems to be 16–18 °C. The population of *E. gracilis* is mainly represented with juvenile individuals. Scarce occurrence of adults (particularly big egg-carrying females) indicates the pressure of fish. In L. Peipsi, the mean average length of juvenile forms is 0.4–1.0 mm (average wet biomass 0.02 mg), that of males 0.9–1.3 mm (0.04 mg), and that of females 1.0–1.4 mm (0.059 mg). The average biomass of an individual of the population is 0.039 mg. The abundance of *E. gracilis* in L. Peipsi fluctuates in the range of 195–41 000 ind. m^{-3}, biomass 0.008–2.408 g m^{-3}; average values of the vegetation period (from May to October) being 27 200 ind. m^{-3} and 0.141 g m^{-3}, respectively. *E. gracilis* is relatively abundant during the whole vegetation period, but it is a dominant only in autumn when water temperature limits the development of the genus *Daphnia* (particularly *D. cucullata*). The species of the genus *Daphnia* are effective filtrators, and their occurrence maxima are marked by low abundance of algae (Jürgens & Stolpe, 1995; Arner et al., 1998). Individuals of *Daphnia* are not very fastidious about food and are able to consume food objects of different size (including bacteria), which serves as an advantage for them. *E. gracilis*, on the contrary, is characterized by highly selective feeding; it prefers large food objects and cannot feed on bacteria (Lampert, 1992). In the 1950s and 1960s, *E. gracilis* was a

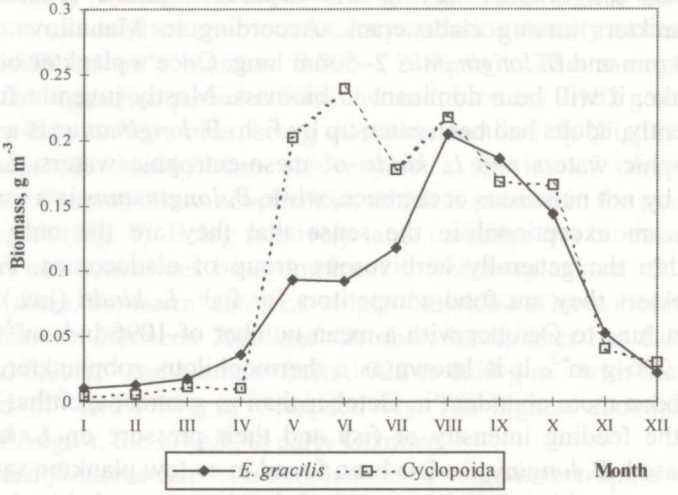

Fig. 8. Biomass of *Eudiaptomus gracilis* and Cyclopoida.

dominant species also in the other large lake, Võrtsjärv, which is connected with L. Peipsi (Schönberg, 1961; Haberman, 1976a), but by now it has practically disappeared from strongly eutrophic L. Võrtsjärv. Decrease in its numbers or even disappearance as a result of increasing eutrophication is a fact known from the literature (Stebler, 1979; Cap, 1980). Also, size-selective feeding of fishes is not favourable for the relatively large *E. gracilis*.

Juvenile forms of copepods (Cyclopoida) are present in L. Peipsi all the year round but in small numbers in winter (Fig. 8). Their number in L. Peipsi ranges from 195 to 272 412 ind. m^{-3} with an average of 20 847 ind. m^{-3}. Biomass fluctuates between 0.001 and 2.977 g m^{-3}, average biomass being 0.178 g m^{-3}. Minima occur in March and maxima in August.

When living conditions in a waterbody (food, water temperature, oxygen regime, trophy, etc.) do not change considerably, the dominant complex of plankton species will remain the same for years. This applies in general also to the zooplankters dominant in L. Peipsi. Comparing the zooplankters that were dominant in the 1960s (Haberman, 1976a, 1976b) with those dominant in the 1980s and 1990s it can be said that the dominant species have been the same in all the periods, while only the degree of domination (%) has changed in case of some species. The species of eutrophic waters have started to dominate more powerfully, while the role of oligo-mesotrophic species has decreased. This is particularly conspicuous in case of rotifers. Domination of rotifers in eutrophic waters and increase in their percentage with rise of the trophy level are well known phenomena. Major changes in zooplankton arise namely from changes in algae. It should be mentioned here that also the phytoplankton species dominant in L. Peipsi have been nearly the same for a long time (more than 30 years) (Laugaste et al., 1996).

ACKNOWLEDGEMENTS

The autor is indebted to the Estonian Science Foundation (grant No. 2015) and to the Estonian Ministry of the Environment for financial support for this investigation. The English text was kindly revised by Mrs. E. Jaigma.

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PEIPSI JÄRVES DOMINEERIVAD ZOOPLANKTERID

Juta HABERMAN

Zooplankton on põhitoiduks planktonitoidulistele kaladele (Peipsis tint ja rääbis) ning kõikide kalade maimudele. Seega on zooplankton veekogu toiduahela keskne ning oluline lüli, millest suurel määral oleneb vetikate loodud orgaanilise aine (energia) transport veekogu toiduahela lõpp-produkti – kalasse. Peipsi on Euroopas üks kalarikkamaid järvi, aastane kalatoodang on 25–31 kg ha^{-1}. Järelikult elutseb järves võimas zooplanktoni kooslus, mis ei lase kaladel nälgida ning annab võimaluse selliseks kalatoodanguks. Viimast väidet kinnitavad ka suured tindisaagid, mis on alates 1930. aastatest olnud enamasti 1500–3500 t aastas. Zooplanktoni kooslust saab kõige paremini iseloomustada domineerivate liikide abil. Dominandiks peetakse liiki (vormi), mis moodustab 20% või enam kogu zooplanktoni arvukusest või biomassist. Arvukuselt domineerivad kogu aasta arvukad, kuid väga väikesed keriloomad, biomassilt aga tunduvalt suuremad vesikirbulised e. kladotseerid ja aerjalalised e. kopepoodid. Järves arvukad oligo-mesotroofsete vete liigid (*Conochilus hippocrepis*, *C. unicornis*, *Kellicottia longispina*, *Bosmina berolinensis*) näitavad järve suhteliselt head, mõõdukalt eutroofset seisundit. Samal ajal aga tuletavad eutroofsete vete karakterliigid (*Keratella cochlearis*, *Daphnia cucullata*, *Bosmina c. coregoni*) meelde, et tegu on siiski eutroofse järvega. Eutroofsuse indikaatorite *Anuraeopsis fissa* ja *Keratella tecta* ajutine ohtrus on lausa ohusignaaliks. Peipsi järve kalatoidu suhteliselt kõrget kvaliteeti näitab see, et zooplanktoni biomassi moodustavad suured kladotseerid (*Daphnia galeata*, *Bosmina berolinensis*, *Limnosida frontosa*, *Diaphanosoma brachyurum* jt.) ning üks suuremaid kopepoode – *Eudiaptomus gracilis*. Kalad ei raiska energiat väikeste toiduobjektide tagaajamisele, vaid toituvad alati selektiivselt, valides suuremaid toiduobjekte. Rohkem kui 30 aasta jooksul ei ole dominantide koosseis Peipsi järves muutunud. Küll aga on muutunud mõnede liikide ülekaalu määr (%). Eutroofsete vete liikide osa (%) on zooplanktonis kasvanud, kuid oligo-mesotroofsete vete liikide oma kahanenud.