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LAKE PEIPSI AND ITS ECOSYSTEM

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Abstract. Lake Peipsi (3555 km^2, mean depth 7.1 m), consisting of three parts (L. Peipsi *s.s.*, L. Pihkva, L. Lämmijärv), is located on the border of Estonia and Russia. L. Peipsi *s.s.* belongs to unstratified eutrophic lakes with mesotrophic features, L. Lämmijärv has some dyseutrophic features, while L. Pihkva is a typical unstratified eutrophic lake. The mean concentrations of total phosphorus and nitrogen in the surface water were 42 and 768 mg m^{-3}, respectively. Biomass of phytoplankton fluctuated between 1 and 125 g m^{-3}, that of zooplankton from 0.088 to 6.344 g m^{-3}, with a summer average of 3.092 g m^{-3}. The total count of bacteria in L. Peipsi *s.s.* was 2.2 × 10^6, in L. Pihkva 4.3 ×10^6, and in L. Lämmijärv 3.9 × 10^6 cells mL^{-1}. The average abundance of macrozoobenthos (without big molluscs) was 2671 ind. m^{-2}, their biomass being 12.9 g m^{-2}. The respective figures for big molluscs (mostly *Dreissena polymorpha*) were 312 ind. m^{-2} and 244 g m^{-2}. Macroflora occupies approximately 5–7.9% of the total area of the lake and is rich in species (129 taxa). Dominant are typical species of eutrophic lakes. The main commercial fishes are dwarf smelt, pikeperch, ruffe, roach, bream, pike, and until the early 1990s also vendace. The total catch of fish has usually been 9000–11000 t (25–31 kg ha^{-1}) a year.

Key words: Lake Peipsi, morphometry, hydrochemistry, biota.

GENERAL FEATURES OF LAKE PEIPSI

Lake Peipsi, or Lake Peipsi–Pihkva (Pskovsko-Chudskoe ozero in Russian, 3555 km^2), is located on the Russian–Estonian border and is the fifth largest lake in Europe. The lakes with a larger area are Ladoga (18 390 km^2) and Äänisjärv or Onega (9840 km^2) in Russia, Väner (5545 km^2) in Sweden, and Saimaa (4400 km^2) in Finland. Lake Peipsi is connected with the sea by the Narva River (77 km) and with another large Estonian lake, Võrtsjärv, by the Emajõgi River (101 km). The catchment basin of L. Peipsi together with the lake surface area covers 47 800 km^2, is of oblong shape, and stretches 370 km from north to south (Fig. 1). Nearly a third of the catchment area is on the Estonian territory and two-thirds, on the Russian territory. Almost 4500 lakes are located in the catchment area, all of them small (less than 1 km^2) except L. Võrtsjärv.

Peipsi is a relatively shallow lake consisting of three parts: the northern, largest and deepest L. Peipsi *s.s.* (*sensu stricto*, also L. Peipus in the older literature, Chudskoe ozero in Russian), southern L. Pihkva (Pskovskoe ozero), and small and narrow L. Lämmijärv (Teploe ozero) connecting the first two (Fig. 2). Table 1 presents basic morphometric data on the lake. Of the 3555 km^2 surface area, 1570 km^2 belongs to Estonia: 1442 km^2 or 55% of L. Peipsi *s.s.*, 118 km^2 or 50% of L. Lämmijärv, and 10 km^2 or 1.3% of L. Pihkva. The volume of L. Peipsi is 25.07 km^3 and water turnover time is about two years. Lake Peipsi *s.s.* is the deepest part of the lake, with 80% deeper than 6 m. The shoreline is not idented – the only bay, Raskopel, is situated in the southeastern part of the lake. The boundary between L. Peipsi *s.s.* and L. Lämmijärv runs along the Meerapalu (Uhtinina)–Piirissaar–Podborov'e line. The boundary is natural, proceeding along a shallow underwater ridge where the water depth is even less than 1 m in some places. In winter, the ice in this area may be dangerously thin. L. Peipsi is connected with L. Lämmijärv by shallow sounds to the west and to the east of Piirissaar Island, which bear the names the Estonian Gates and the Russian Gates, respectively. A dredged shipping track, with a length of 2.5 km, width of 60 m, and depth of 2 m, passes through the Estonian Gates. Lake Lämmijärv is generally shallow, with an average depth of 2.5 m. However, it is namely in L. Lämmijärv, in its narrowest part (1.8 km) at Mehikoorma, where the deepest point of L. Peipsi (15.3 m) is located. The name of L. Lämmijärv (Warm Lake) is hydrologically justified: in spring and in winter the water in L. Lämmijärv is much warmer than in L. Peipsi *s.s.* or in L. Pihkva. In winter the thin water layer of L. Lämmijärv warms up to the ice cover, while in deeper L. Peipsi *s.s.* warming up in winter is restricted only to a few near-bottom metres. In spring, owing to its shallowness, L. Lämmijärv warms up faster than the water mass of L. Peipsi *s.s.* In summer L. Lämmijärv is also warmer than the other lake parts; in autumn, cooling down takes less time. Lake Pihkva is separated from L. Lämmijärv by the line connecting the western shore of Värska Bay and Mtezh. Lake Pihkva is considerably smaller and shallower than L. Peipsi *s.s.* (Table 1) and similar to L. Lämmijärv with respect to the temperature regime (Table 2). The northwestern corner of the lake is the site of Värska Bay.

There are more than 30 islands in L. Peipsi. The largest are Kolpino (11.1 km^2), Piirissaar (7.5 km^2), and Kamenka (4 km^2) off the western coast of L. Pihkva. A group of three islands, Talabski, situated near the eastern coast of L. Pihkva, is a special sight. The total area of the islands is 27.2 km^2, forming 0.8% of the surface area of the lake.

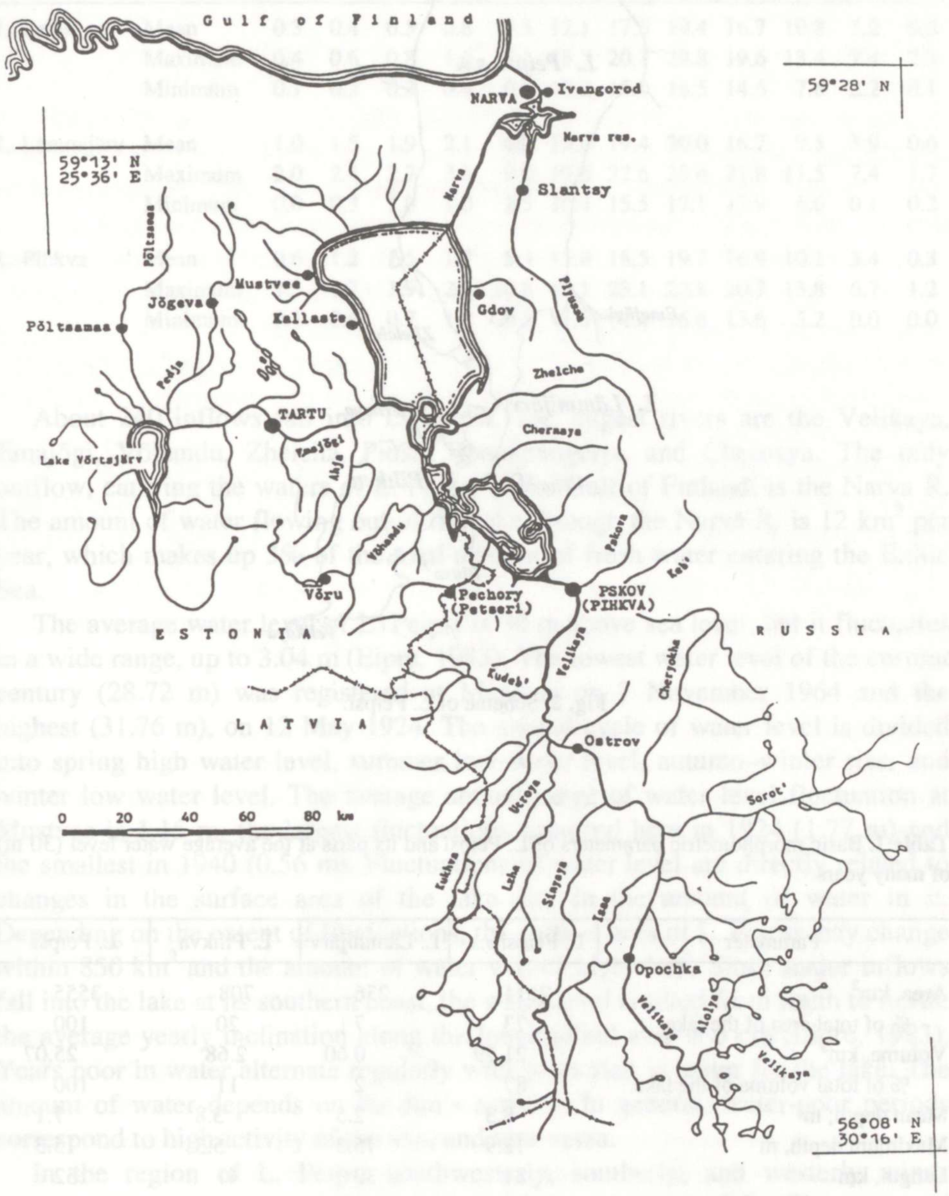

Fig. 1. Catchment area of L. Peipsi (Jaani & Raukas, 1999, p. 10).

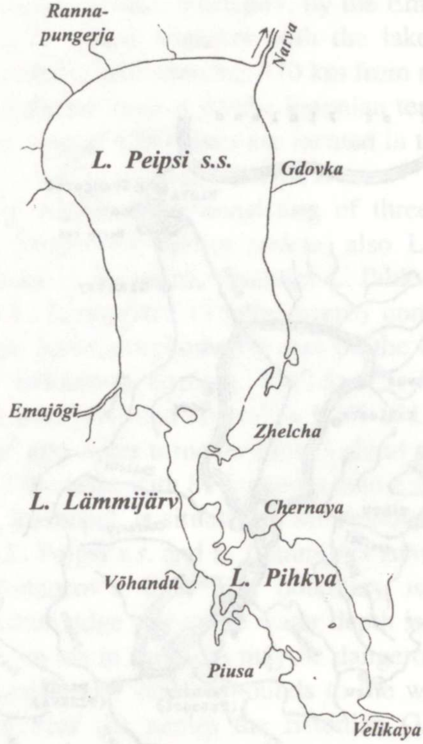

Fig. 2. Scheme of L. Peipsi.

Table 1. Basic morphometric parameters of L. Peipsi and its parts at the average water level (30 m) of many years

Parameter	L. Peipsi *s.s.*	L. Lämmijärv	L. Pihkva	L. Peipsi
Area, km^2	2611	236	708	3555
% of total area of the lake	73	7	20	100
Volume, km^3	21.79	0.60	2.68	25.07
% of total volume of the lake	87	2	11	100
Mean depth, m	8.3	2.5	3.8	7.1
Maximum depth, m	12.9	15.3	5.3	15.3
Length, km	81	30	41	152
Mean width, km	32	7.9	17	23
Maximum width, km	47	8.1	20	47
Length of shoreline, km	260	83	177	520
% of total length of shoreline	50	16	34	100

Table 2. Water temperatures (°C) of L. Peipsi during 1958–75 (Uleksina & Filatova, 1983)

		1.01	1.02	1.03	1.04	1.05	1.06	1.07	1.08	1.09	1.10	1.11	1.12
L. Peipsi *s.s.*	Mean	0.3	0.4	0.5	0.8	3.5	12.1	17.6	19.4	16.7	10.8	5.2	0.8
	Maximum	0.4	0.6	0.8	1.6	6.1	13.7	20.1	22.8	19.6	13.4	7.4	2.3
	Minimum	0.1	0.3	0.3	0.4	0.9	10.2	15.0	16.5	14.6	7.6	2.2	0.1
L. Lämmijärv	Mean	1.0	1.5	1.9	2.1	6.0	15.0	19.4	20.0	16.7	9.5	3.9	0.6
	Maximum	2.0	2.4	2.7	3.6	9.0	19.6	22.6	23.6	21.8	11.5	7.4	1.7
	Minimum	0.0	0.3	1.0	1.0	2.5	10.4	15.5	17.1	13.9	6.6	0.1	0.2
L. Pihkva	Mean	0.6	1.2	1.5	1.7	5.4	15.0	18.5	19.7	16.9	10.1	3.4	0.3
	Maximum	1.3	1.7	1.9	2.3	10.8	19.1	23.1	22.8	20.7	13.8	6.7	1.2
	Minimum	0.1	0.6	0.7	1.2	0.5	11.5	14.4	16.6	13.6	5.2	0.0	0.0

About 240 inflows fall into L. Peipsi. The largest rivers are the Velikaya, Emajõgi, Võhandu, Zhelcha, Piusa, Rannapungerja, and Chernaya. The only outflow, carrying the waters of L. Peipsi to the Gulf of Finland, is the Narva R. The amount of water flowing out of the lake through the Narva R. is 12 km^3 per year, which makes up 3% of the total amount of fresh water entering the Baltic Sea.

The average water level of L. Peipsi is 30 m above sea level, but it fluctuates in a wide range, up to 3.04 m (Eipre, 1983). The lowest water level of the current century (28.72 m) was registered at Mustvee on 7 November 1964 and the highest (31.76 m), on 12 May 1924. The annual cycle of water level is divided into spring high water level, summer low water level, autumn–winter rise, and winter low water level. The average annual range of water level fluctuation at Mustvee is 1.15 m; the largest fluctuations occurred here in 1924 (1.77 m) and the smallest in 1940 (0.56 m). Fluctuations of water level are directly related to changes in the surface area of the lake and in the amount of water in it. Depending on the extent of fluctuations, the surface area of L. Peipsi may change within 850 km^2 and the amount of water within 11.15 km^3. Since major inflows fall into the lake at its southern coast, the water level is tilted from south to north: the average yearly inclination along the longitudinal axis is 8 cm (Eipre, 1983). Years poor in water alternate regularly with years rich in water for the lake. The amount of water depends on the sun's activity. In general, water-poor periods correspond to high activity of the sun, and vice versa.

In the region of L. Peipsi southwesterly, southerly, and westerly winds prevail. The windiest month is October, and the calmest is July. The waves of L. Peipsi are short and sharp, which is characteristic of shallow lakes. At the dominating wind speed of 5 m s^{-1} in summer, the wave height in L. Peipsi *s.s.* is 40–60 cm, in L. Lämmijärv 20–30 cm, and in L. Pihkva 30–40 cm. The height of waves reaches rarely 75–100 cm (Veering & Chudnova, 1983). The highest waves were registered in 1961 and 1962 with a wind speed of up to 20 m s^{-1}. It is generally known that going in the boat on the lake is dangerous at wind speed higher than 5 m s^{-1}.

The first ice near the coast is usually formed in early November. Freezing starts in shallow, more rapidly cooling lake parts, and by mid-December the whole lake is usually covered with ice. The ice cover attains the largest thickness by the end of March: on average 60 cm, sometimes even more than 1 m. Ice is thinner in the vicinity of the mouth of the Emajõgi R., in the Estonian and Russian Gates, and in Värska Bay. The area around the outflow of the Narva R. is for the most part ice-free until spring and freezes over only during very cold periods. Shortly after the ice cover is formed cracks appear, mostly 1–2 m in width. However, there exist data on a crack with a width of 8 m in the northern part of L. Peipsi *s.s.* (Jaani & Raukas, 1995). With thin ice and snow, cracks may present hazard to people walking on the ice. Ice starts to break in L. Lämmijärv in early April, and in L. Pihkva and L. Peipsi *s.s.* in mid-April. Usually, the whole lake becomes ice-free by the end of April, but in some years ice has been found in the northern part of the lake as late as the end of May.

Water temperatures in Lake Peipsi are characterized by Table 2. Water is the warmest in July–August, while its temperature in shallower lakes Lämmijärv and Pihkva is higher than in larger and deeper L. Peipsi *s.s.* (Uleksina & Filatova, 1983).

THE ECOSYSTEM OF LAKE PEIPSI

Chemical composition of water

The chemical composition of the water of L. Peipsi was studied by the Hydrometeorological Service over the period 1950–91, by the hydrochemistry team of the Institute of Zoology and Botany during 1985–92, and by the South Estonian Laboratory of Environmental Protection at the Ministry of the Environment in the 1990s. The highest pollution load with 14.6 g m^{-2} of nitrogen and 0.80 g m^{-2} of phosphorus (load on surface) is received by L. Pihkva, followed by L. Lämmijärv with 9.0 and 0.27 g m^{-2} and L. Peipsi *s.s.* with 2.5 and 0.09 g m^{-2}, respectively (Loigu et al., 1991). Annually 3600 t of nitrogen and 30 t of phosphorus reach the lake surface directly from the air. The overall mean concentrations of total phosphorus and nitrogen in the surface water of L. Peipsi were 42 mg P m^{-3} and 768 mg N m^{-3} during the period of 1985–96. The northern part of the lake (L. Peipsi *s.s.*) is significantly poorer in P and N compounds than the southern part (L. Pihkva), which is affected by pollution from the Velikaya R. Taking the P and N concentrations in Estonian small lakes (Milius et al., 1991, 1994) as basis for assessing the trophic state of the three parts of L. Peipsi we can see clear differences: L. Pihkva is hypertrophic, the state of L. Lämmijärv is close to hypertrophic, but L. Peipsi *s.s.* is a eutrophic waterbody. The concentrations of P and N show a decreasing trend from south to north (difference between the southern tip of L. Pihkva and the northern tip of

L. Peipsi *s.s.* is about twofold). The concentration of phosphate ions (PO_4^{3-}) was significantly higher in 1959–84 (overall mean 18 mg P m^{-3}) than in 1985–96 (8 mg P m^{-3}). In 1985–96 PO_4^{3-} formed 20–25% of total phosphorus. The concentration of nitrate as well as nitrite ions was, on the contrary, lower in 1953–84 (overall mean 14 and 1.6 mg N m^{-3}) than in 1985–96 (32 and 2.8 mg N m^{-3}, respectively). Such concentrations are characteristic of natural surface waters. In 1970–84, the level of the ammonium ion was significantly higher (overall mean 178) than in 1985–96 (22 mg N m^{-3}). The mean concentrations of silicon and total iron over the lake were 0.7 and 0.10 mg L^{-1}, respectively, in 1985–96.

The water of L. Peipsi is rich in oxygen, mostly slightly under- or over-saturated with O_2. In 1985–96, the O_2 concentration was usually 7.7–13 mg L^{-1}, and oxygen saturation was 86–117%. The overall mean concentration of O_2 was 10 mg L^{-1} and mean saturation 100%. The water of L. Peipsi is slightly alkaline: the mean pH during the years 1985–96 was 8.28.

The range of water colour of L. Peipsi is broad, from dark reddish brown to light green. The darkest water, mostly brownish yellow, is in L. Pihkva. The water of L. Lämmijärv is greenish or brownish yellow and the water of L. Peipsi *s.s.* is the lightest, often yellow or greenish yellow. During 1985–96, the water colour was commonly 23–56°, with an overall mean of 35°. The total content of organic matter is characterized by dichromate oxidizability (COD_{Cr}) and the easily oxidized fraction (mainly humic matter) by permanganate oxidizability (COD_{Mn}). In 1985–96, the mean COD_{Cr} and COD_{Mn} were 30 and 13 mg O L^{-1}, respectively. The content of organic matter decreases from south to north over the whole lake. The range of water transparency (SD) was broad. In 1985–91, SD was mostly 1.0–3.4 m, with an overall mean of 1.9 m. In the northern part of the lake SD was about three times as high as in the southern part.

According to its hydrochemical characteristics the water of L. Peipsi belongs to the Ca group of the hydrogen carbonate class. The ionic composition of water is dominated by HCO_3^-, followed by SO_4^{2-} and Cl^-. The first place among cations is occupied by Ca^{2+}, followed by Mg^{2+}, Na^+, and K^+ (Starast et al., 1999). Specific changes took place in the ionic composition in the middle of the 1960s. The proportion of HCO_3^- and Ca^{2+} decreased over the years, whereas the importance of SO_4^{2-}, Na^+, K^+, and Cl^- ions, reflecting anthropogenic impact, increased. The mean total alkalinity of L. Peipsi was 2.25 meq L^{-1} or 137 mg HCO_3^- L^{-1} during 1985–96. In the earlier study period (1950–84), as compared with the later period (1985–96), the mean concentrations of SO_4^{2-} and Cl^- over the lake were essentially lower, respectively 0.41 and 0.19 against 0.51 and 0.27 meq L^{-1}. The content of Ca^{2+} and Mg^{2+} varied relatively little, being 1.89 and 0.99 meq L^{-1}, respectively, in 1985–96.

Phytoplankton

The phytoplankton of L. Peipsi is singular and opulent: it consists of about 500 algal species, and this number will increase when all collected data are systematized. Besides common eutrophic algae, mesotrophic species as well as arctic, halophilous, halophobous, acidophilous, and alkaliphilous species occur. In different seasons and years, 36 main species (dominants and subdominants) form 68–96% of the biomass in more eutrophic L. Pihkva and 60–97% in less eutrophic L. Peipsi *s.s.* Lake Lämmijärv is similar to L. Pihkva in respect to phytoplankton and the trophic state. Diatoms and blue-green algae predominate in biomass, while diatoms and green algae predominate in the species number. The oligo-mesotrophic *Aulacoseira islandica* (O. Müller) Sim. is characteristic of the cool period; *A. granulata* (Ehr.) Sim. and *Stephanodiscus binderanus* (Kütz.) Krieger prevail in summer and autumn, the latter being most abundant in the southern part. *Gloeotrichia echinulata* (J. S. Smith) P. Richter and *Aphanizomenon flos-aquae* (L.) Ralfs dominate in summer, causing water-blooms. In early spring and autumn *A. islandica* causes strong water-blooms every four to six years. Phytoplankton has mostly three maxima in the seasonal dynamics of L. Peipsi *s.s.* and one or two of L. Pihkva. In different years its spring biomass has fluctuated in the range 2–16 g m^{-3} in L. Peipsi *s.s.* and in the range 1–8 g m^{-3} in L. Pihkva and L. Lämmijärv. The respective figures for summer are 3–17 and 6–125 (in most cases 15–25) g m^{-3}, and for autumn, 7–20 and 5–35 g m^{-3}. The dominant complex has not changed considerably since 1909; however, the distribution of dominant species in lake parts has become more even in recent decades. A series of quantitative summer data shows quite large fluctuations, evidently connected with water level: phytoplankton biomass was larger in years with low water level. In the course of the studied 36 years, the southern parts of the lake have become strongly eutrophic, but L. Peipsi *s.s.* has eutrophied to a smaller extent and has maintained its mesotrophic appearance. However, the fluctuations in the biomass and chlorophyll content have become sharper, and their peaks higher and more frequent. The species that require highly eutrophic conditions are becoming increasingly more widespread.

Bacterioplankton

The first water samples from L. Peipsi for microbiological analysis were collected by A. Mäemets in 1962. Systematic investigations have been carried out on the lake since 1980. Water samples for microbiological studies were gathered on the summer expeditions of 1980, 1982, and 1984–87. In connection with comprehensive investigations, microbiological analyses of the major inflows (11 rivers) and the outflow of L. Peipsi as well as of the open part of the lake were made in 1985–87. Since 1992 microbiological monitoring is part of the monitoring programme of the Estonian part of L. Peipsi. According to the data of 1980–87 the total count of bacteria in L. Peipsi *s.s.* was on average 2.2×10^6 cells mL^{-1}. In L. Pihkva and L. Lämmijärv the concentration of bacteria was higher, 4.3×10^6 and 3.9×10^6 cells mL^{-1}, respectively (Lokk & Kisand, 1996). The total count of bacteria revealed three rises during the period of investigations: at the beginning of the 1980s in all lake parts, in 1984–86 in L. Lämmijärv and L. Pihkva, and, following a decrease in 1992, in 1993–95 in L. Lämmijärv. Fluctuations were more significant in case of L. Pihkva and L. Lämmijärv, which represent almost typical Estonian eutrophic lakes (Lokk & Kisand, 1999).

In different years, the average number of saprophytic bacteria ranged from 110 to 360 cells mL^{-1} in L. Pihkva and L. Lämmijärv and from 98 to 290 cells mL^{-1} in L. Peipsi. The highest saprophytic bacteria numbers (up to 5900 cells mL^{-1}) were determined in the mouths of the rivers Velikaya and Emajõgi. The determination of total coliform, the number of *Enterococci*, as well as the numbers of saprophytic bacteria indicated that the pelagial of L. Peipsi was in a good sanitary state. The maximum of total coliforms for the pelagial, 240 per 100 mL, occurred in areas under the impact of inflows. *Enterococci* were found near the inflows of rivers (up to 27 cells in 10 mL of water), but not in the open water.

The total count of bacteria in the inflows of L. Peipsi ranged from 3.0×10^6 to 11.9×10^6 cells mL^{-1}. Estimation of seasonal changes in inflows revealed an increase in the total count of bacteria and of saprophytic bacteria in spring and autumn. The former is probably caused by the inflow of allochthonous substances with high water, the latter by decomposition of organic matter and increased precipitation. Analyses indicated that the total count of bacteria and the average number of saprophytic bacteria were in many cases the highest in winter. The coliform count in the rivers remained quite uniform during the whole period; still, in spring the number of analyses that did not satisfy sanitary requirements was greater. The density of bacteria in the outflowing Narva R. was low, ranging between 1.4×10^6 and 4.1×10^6 cells mL^{-1}.

Zooplankton

The zooplankton of the lake has been studied since 1909, i.e. for 90 years. Altogether 268 zooplankton taxa have been identified from the pelagial of the lake (Haberman, 1971; Mäemets et al., 1996; Virro, 1996). The species whose numbers and biomass amount to 20% or more of total zooplankton 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) dominants included also species preferring eutrophic waters (*Keratella cochlearis* (Gosse), *Daphnia cucullata* Sars, *Bosmina c. coregoni* Baird, sometimes even *Anuraeopsis fissa* (Gosse) and *Keratella tecta* (Gosse)). The number of zooplankton fluctuates between 46×10^3 and 2752×10^3 ind. m^{-3}; biomass ranges from 0.088 to 6.344 g m^{-3}, with the summer average of 3.092 g m^{-3}.

The importance of rotifers in zooplankton is great: they dominate all the year round in number (74%), although their proportion in the biomass of zooplankton is small. Cladocerans are practically absent from winter plankton. Mass development of cladocerans starts in June (water temperature 16.5 °C) when they make up 6% of the zooplankton number and 32% of the biomass. They reach their maximum proportion in the zooplankton in autumn, in October–November, when they constitute on an average 21% of the number and 56% of the biomass. Copepods occupy an important position in L. Peipsi the whole year, accounting for an average of 16% of the number and 35% of the biomass. The proportion of *Dreissena polymorpha* (Pallas) larvae is insignificant in the zooplankton biomass (< 1%) but sometimes rather important in their number (up to 10%). The seasonal pattern of the dynamics of the zooplankton number has two peaks (in May and August), both of which are built up of rotifers. The biomass has a distinct peak in July and a small rise in October, both on account of cladocerans: in July mainly the genus *Daphnia*, in October the genus *Bosmina*. The trends of the seasonal dynamics of the number and biomass are not synchronous, especially in May and August when plankton are dominated by small rotifers, and in October–November when *Bosmina berolinensis* Imhof, *Daphnia galeata* Sars, *Eudiaptomus gracilis* (Sars), and Cyclopoida are prevailing. In comparison with the 1960s and 1970s (Mäemets, 1966; Haberman, 1971; Ibneeva, 1980), no definite changes have occurred in zooplankton biomass; however, their number has increased due to the larger proportion of rotifers, whose effect on biomass is weak. Such a tendency accompanies a rise in the trophic level.

The production of herbivorous zooplankton fluctuates between 0.05 and 5.9 g C m^{-2} $month^{-1}$; the production of predators between 0.002 and 0.69 g C m^{-2}; the production of the whole zooplankton community was 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). According to Ibneeva (1980) herbivorous crustaceans produced 16.4 and predatory crustaceans 2 g C m^{-2} in L. Peipsi during the vegetation period in 1976–78. The production of herbivorous zooplankton constituted 10.1% of primary production in L. Peipsi. This percentage indicates a direct relationship between zoo- and phytoplankton; filtrators feed mostly on living algae and the detrital food chain is of little importance. The herbivorous zooplankton ration (0.55 ± 0.14 g C m^{-2} d^{-1}) constituted about 50% of the daily primary production, which was 1.1 ± 0.1 g C m^{-2} (Nõges et al., 1993). High grazing efficiency (50%) in L. Peipsi is caused by domination of efficient filtrators (*D. galeata, B. berolinensis, E. gracilis*) in the lake.

Both planktophagous fishes and predatory zooplankton feed on zooplankton. The most essential predators in the zooplankton of L. Peipsi are adults and juveniles of stages IV and V *Mesocyclops* (mainly *M. leuckarti* (Claus) and

M. oithonoides (Sars)), *Bythotrephes longimanus* Leydig, *Leptodora kindti* (Focke), *Heterocope appendiculata* Sars, and *Asplanchna priodonta* Gosse. Predatory zooplankton consumed on an average 50% of the production of filtrative zooplankton. The proportion of zooplankton production reaching fishes was also about 50%. An average of 6% of the energy of primary production reaches fishes. This supports the conclusion that the lake's food web is rather efficient.

Zoobenthos

Since 1964, annual zoobenthos studies with the same sampling network and methods have been carried out on L. Peipsi by the staff of the Võrtsjärv Limnological Station. For estimating the abundance and biomass of macrozoobenthos, L. Peipsi was monitored at 22–24 sampling sites in early June since 1964 to 1992. From then on sampling was continued at 11–13 sites on the Estonian aquatory only. Shallow-water monitoring was carried out in the midsummer (July–August) of 1970, 1980, and 1990 at 50 profiles along the whole shoreline. All samples were taken by a Borutskij or Zabolotskij type grab sampler with a 225 cm^2 grasp area with three hauls per sample. Ethanol-fixed wet weight was used in calculations.

At least 421 species and forms of bottom animals have been found in L. Peipsi (Timm et al., 1996a). Among these Chironomidae occupy the first place with about 111 taxa, followed by Mollusca (83) and Oligochaeta (59). Species characteristic of eutrophic waters are dominating in the lake. No qualitative changes were observed in the bottom fauna during the last 35 years, except for the introduction of a Baikalian gammarid species, *Gmelinoides fasciatus* (Stebbing) (Timm et al., 1996b). Neither essential changes in the specific composition of bottom fauna nor shifts in the distribution of benthic communities were noted during the study period. Dominant species also remained the same in all benthic zones.

In L. Peipsi the mean (± standard error) macrozoobenthos abundance was 2671 ± 132 ind. m^{-2} and biomass 12.95 ± 0.71 g m^{-2} in June 1964–98. The values for different sampling sites showed considerable differences. Chironomids outweighed all the other bottom animals combined (excluding big clams) with respect to biomass (57% of the total biomass), but came second after oligochaetes with respect to abundance (Kangur, 1999). Oligochaetes were also the most abundant taxonomic group of macrozoobenthos in the lake (about 44% of its total abundance). Considering biomass, oligochaetes came second (17% of the total biomass). The abundance of small molluscs (Gastropoda, Pisidiidae) and other small animals was considerably lower than that of chironomid larvae and oligochaetes. The abundance of large molluscs (Unionidae, *Viviparus*, and particularly *Dreissena*) was high, with an average of 312 ± 48 ind. m^{-2}. Their biomass (average 244 ± 33 g m^{-2} in 1964–98) was about twenty times as large as the total biomass of all other macrozoobenthos. *Dreissena polymorpha* (Pallas), introduced accidentally in the lake in the 1930s, formed extensive banks in the sublittoral and represented the most important animal population in the lake.

According to its macrozoobenthos, L. Peipsi is a well-preserved eutrophic lake with some mesotrophic features supported by its large water mass and strong wind disturbance (Timm et al., 1996a). Its profundal (bare soft mud bottom) fauna consists only of animals characteristic of eutrophic lakes with *Chironomus plumosus* (L.) and *Potamothrix hammoniensis* (Mich.) as the dominants. In the sublittoral and, particularly, in the littoral, the bottom fauna revealed large in-lake variations. Besides typical eutrophic species, several species characteristic of oligotrophic lakes or flowing water were found on wave-exposed sandy bottom. The phytophilous fauna was limited only to small sheltered areas.

The average total biomass in June (without big molluscs) showed considerable annual fluctuations. A significant increase was observed in the biomass of the big clam *D. polymorpha*. Variation in the total macrozoobenthos biomass in L. Peipsi as well as in the other large eutrophic lake in Estonia, Võrtsjärv, depended mainly on the dominant species of the profundal, *C. plumosus* (Kangur et al., 1998). Despite the fluctuations, the community demonstrated notable stability in overall abundance and biomass over the years: low abundance in some years was followed by fast recovery of the previous level.

Lake Peipsi appears to be the richest in macrozoobenthos among the North European large lakes (Timm et al., 1996a). However, the ample macrozoobenthos resources, which are the principal food of benthophagous fishes, are underconsumed in the lake. The abundance of benthophagous fishes is low compared with L. Võrtsjärv, where eel, bream, and ruffe are very abundant (Kangur et al., 1999). In L. Peipsi eel is represented only with a few specimens. The population density of bream could be higher, but suitable spawning grounds are restricted for this fish. Ruffe is the most numerous benthophagous fish in L. Peipsi. As ruffe and bream have favourable feeding conditions, both their growth rate and condition factor are high compared with the respective parameters for other Estonian lakes.

Fishes

According to current data one lamprey and 33 fish species inhabit permanently L. Peipsi or the lower reaches of its tributaries (Pihu, 1996). Regarding the amount of catches the main commercial fishes are dwarf or lake smelt, *Osmerus eperlanus eperlanus* m. *spirinchus* Pallas (its annual catch in the lake has been usually 1500–3000 t), perch (100–1700 t), pikeperch (20–200 t, but 920–1360 t in the 1990s), ruffe (500–1500 t), roach (400–600 t), bream (300–600 t), pike (200–400 t), and until the early 1990s also vendace (300–1500 t, but 45–167 t in 1995–98). Burbot, whitefish, and white bream are of less importance as commercial fishes. The total catch has usually been 9000–11 000 t (25–31 kg ha^{-1})

per year. About 40–50% of the catch belongs to Estonia, the rest to Russia. In general, the spawning and feeding conditions of fishes in the lake are more or less favourable. The stock of dwarf smelt suffered seriously for summer anoxia twice (in 1959 and 1972) but it was restored in two to four years (Kuderskij & Fedorova, 1977).

Earlier L. Peipsi was regarded as a smelt–bream lake, but from the second half of the 1980s it has obtained also some features of a pikeperch lake. As a result of intensive use of trawls and fine-meshed Danish seines the stock of pikeperch in the lake was strongly suppressed for a long time (1957–82). Owing to the demands of both Estonian and Russian ichthyologists trawls were prohibited and the number of Danish seines was considerably reduced (from 133 to 40). As a result the stock and catches of pikeperch began to grow rapidly and soon it became one of the most important commercial fishes in the lake.

In recent years the abundance and catches of vendace have decreased sharply in L. Peipsi. This is probably due to the high mortality of its eggs on the spawning grounds during successive mild winters in the late 1980s and early 1990s, when the lake had no permanent ice cover and the bottom was in places exposed to the action of waves. Thanks to the normal winters of recent years (1994–99) the stock of vendace is gradually restoring.

It has been recommended to begin regular introduction of elvers into L. Peipsi, at a rate of at least 10 million individuals per year.

Macrovegetation

In the late 1980s, macrovegetation covered 7.5 and 7.9% of the surface area of L. Lämmijärv and L. Pihkva, respectively (Sudnitsõna, 1990). As regards L. Peipsi *s.s.*, recent data are lacking; presumably vegetation occupies there up to 5% of the surface area. Character species of large eutrophic lakes are dominating: *Phragmites australis* (Cav.) Trin., *Schoenoplectus lacustris* (L.) Palla, and *Potamogeton perfoliatus* L. Other frequent species include *P. gramineus* L., *P. pectinatus* L., *Polygonum amphibium* L., *Eleocharis palustris* (L.) Brown, *Sagittaria sagittifolia* L., *Butomus umbellatus* L., *Sium latifolium* L., and *Carex* spp. The list of species comprises 129 taxa, of which 44 are hydrophytes, i.e. submergent plants and floating-leaved and floating plants. *Subularia aquatica* L. and *Isoëtes setacea* Lam. have disappeared during recent decades, while a number of plants that were earlier quite common in shallower littoral regions, such as *Alisma gramineum* C. Ch. Gmel., *Potamogeton filiformis* Pers., *P. panormitanus* Biv. Bern., and some others, seem to be endangered. The main cause is continuous expansion of reeds both lengthwise along the shore and in width, their denser growth, and the consequent paucity of shore stretches free of vegetation; decrease in water transparency also plays a certain role. During the period of the most intensive eutrophication, from the end of the 1960s to the end of the 1980s, the productivity of dominant species changed significantly. Bioproduction increased particularly for reed (7–39 times) and decreased most notably for *Potamogeton perfoliatus* (4–7 times) (Sudnitsõna, 1990). The average growth depth for submergent plants has decreased from 2–3 to 1.5–2 m (Tuvikene, 1966; Sudnitsõna, 1990).

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PEIPSI JÄRVEST NING SELLE ELUSTIKUST

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Peipsi järv e. Peipsi–Pihkva järv (3555 km^2) paikneb Eesti–Vene piiril ning on Euroopas suuruselt viies järv. Soome lahega ühendab Peipsi järve Narva jõgi (77 km) ning teise suure Eesti järve Võrtsjärvega Emajõgi (101 km). Peipsi järve valgala koos järve pindalaga on 47 800 km^2. Peipsi järv koosneb kolmest osast: kõige põhjapoolsemast, suurimast (2611 km^2) ja sügavaimast (keskmine sügavus 8,3 m, suurim sügavus 12,9 m) Peipsist *s.s.* (*sensu stricto*), lõunapoolsest Pihkva järvest (708 km^2, keskmine sügavus 3,8 m, suurim sügavus 5,3 m) ning neid ühendavast väikesest ning kitsast Lämmijärvest (236 km^2, keskmine sügavus 2,5 m, suurim sügavus 15,3 m). Peipsi pindalast kuulub Eestile 1570 km^2: 1442 km^2 e. 55% Peipsi *s.s.* järvest, 118 km^2 e. 50% Lämmijärvest ning 10 km^2 e. 1,3% Pihkva järvest. Vett on Peipsi järves 25,07 km^3 ning vesi vahetub umbes kahe aastaga. Peipsis on rohkem kui 30 saart. Suuremad neist on Värska lahes asuv Kolpino saar (11,1 km^2), Piirissaar (7,5 km^2) ja Pihkva järve läänekalda lähedal asuv Kamenka (4 km^2). Peipsil on umbes 240 sissevoolu. Suuremad jõed on Velikaja, Emajõgi, Võhandu, Želtša, Piusa, Rannapungerja ja Tšornaja. Välja voolab aga Peipsist vaid Narva jõgi. Peipsi keskmine veetase on 30 m üle merepinna, kuid veetase kõigub järves märkimisväärse amplituudiga (aasta keskmine 1,15 m, maksimaalne 3,04 m). Detsembri keskpaigast kuni aprilli lõpuni on järv jääga kaetud. Kõige soojem on vesi juulis–augustis (veesamba keskmine temperatuur 17,6–19,7 °C). Suvel valdava tuulekiiruse juures (5 m/s, 3 palli) on laine kõrgus Peipsi *s.s.* järves 40–60, Lämmijärves 20–30 ja Pihkva järves 30–40 cm. Harva on laine kõrgus 75–100 cm.

Olulisemad keskmised hüdrokeemilised andmed Peipsi järve kohta on järgmised: pinnavee fosforisisaldus – 42 mg m^{-3}, lämmastikusisaldus – 768 mg m^{-3}, pH – 8,28, vee läbipaistvus – 1,9 m, hapnikusisaldus – 10 mg l^{-1}, COD_{Cr} – 30 mg O l^{-1}, COD_{Mn} – 13 mg O l^{-1}. Fütoplankton koosneb ligi 500 vetikaliigist; selle biomass kõigub kevadel Peipsi järves 2–16 ja Pihkva järves 1–8 g m^{-3}, suvel vastavalt 3–17 ja 6–125 g m^{-3} ning sügisel 7–20 ja 5–35 g m^{-3}. Keskmine bakterite üldarv on Pihkva järves $4{,}3 \times 10^6$, Lämmijärves $3{,}9 \times 10^6$ ning Peipsi järves $2{,}2 \times 10^6$ rakku ml^{-1}. Saprobakterite arv kõikus Pihkva ja Lämmijärves vahemikus 110–360, Peipsi järves 98–290 rakku ml^{-1}. Zooplanktonis elutsevad kõrvuti oligo-, meso- ja eutroofsete vete liigid ning neid on kokku 268 (Rotatoria – 182, Cladocera – 57, Copepoda – 28, Mollusca – 1 (*Dreissena polymorpha* juv.)). Zooplanktoni arvukus kõigub piirides 46×10^3 kuni 2752×10^3 isendit m^{-3}, biomass 0,088–6,344 g m^{-3}. Suve keskmine biomass on 3,092 g m^{-3}. Pihkva järves on zooplanktonit rohkem kui Peipsi järves. Peipsi põhjaloomastikus on seni teada 421 liiki (näit. Chironomidae – 111, Mollusca – 83, Oligochaeta – 59). Põhjaloomade (suuri limuseid arvestamata) keskmine arvukus on 2671 isendit m^{-2} ja biomass 12,9 g m^{-2}. Suurtaimestik moodustab Peipsi *s.s.* pindalast 5, Lämmijärvest 7,5 ning Pihkva järvest 7,9%. Suurtaimi on senini teada 129 taksonit, domineerivad suurte eutroofsete järvede karakterliigid.

Peipsi tähtsamad tööndusкalad on tint, ahven, koha, kiisk, särg, latikas ja haug ning 1990. aastateni ka rääbis. Kalade aastane kogusaak on tavaliselt olnud 9000–11 000 t (25–31 kg ha^{-1}). Traalide ja peenesilmaliste mutnikute intensiivne kasutamine viis kohavarud pikaks ajaks (1957–1982) madalseisu. Need taastusid pärast traalpüügi keelamist ja mutnikute arvu tunduvat vähendamist. Nüüd on koha järves muutunud üheks tähtsamaks tööndusкalaks. Viimasel kümnendil on rääbise arvukus järves kõvasti langenud, mida on ilmselt põhjustanud eelkõige rääbisemarja suur suremus koelmutel järjestikuste pehmete talvede ajal 1980. aastate lõpul ja 1990. aastate algul. Peipsisse tuleks hakata regulaarselt asustama klaasangerjaid.