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Temporal and spatial variation in the zooplankton : phytoplankton biomass ratio in a large shallow lake

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Abstract. The material of the present study was collected from the pelagial of L. Peipsi (Estonia/Russia) mainly during the vegetation periods of 1997–2008. The zooplankton : phytoplankton biomass ratio (B_{Zp}/B_{Phyt}) was followed in different lake parts: the northern eutrophic L. Peipsi *s.s.* and the southern hypertrophic L. Pihkva (together with L. Lämmijärv connecting the other parts). During 1997–2008 the average values of B_{Zp}/B_{Phyt} for the growing season were lower than 0.5 (0.27 and 0.16 for L. Peipsi *s.s.* and L. Lämmijärv, respectively). The average monthly values of B_{Zp}/B_{Phyt} fluctuated in a wide range: from 0.06 to 0.62 for L. Peipsi *s.s.* and from 0.06 to 0.29 for L. Lämmijärv in May–October. For L. Pihkva, this value was 0.06 in August. Maximum values (up to 2) occurred for L. Peipsi *s.s.* in June and quite a high value (up to 1) was also found in May. In parallel with the increasing trophic state of the lake, the mean values of B_{Zp}/B_{Phyt} for the growing season decreased from 0.34 in 1997 to 0.18 in 2008 in L. Peipsi *s.s.*, and from 0.24 to 0.10 in L. Lämmijärv. The widest range of fluctuations in B_{Zp}/B_{Phyt} was found in May and August. For May this is explicable with differences in the melting time of the ice cover and therefore, in the timing of the spring peak of phytoplankton in different years. In August the absolute values of phytoplankton (water bloom caused by cyanobacteria) varied by years and depended mainly on weather conditions. The ratio demonstrated lowest variability in autumn months. This ratio revealed significant differences in the content of nutrients and characteristic features in plankton between the lake parts with different levels of trophy (P-level <0.0001). We consider mean values of the ratio B_{Zp}/B_{Phyt} in a growing season to be quite a reliable indicator for assessing the quality of the ecosystem and water of a large lake.

Key words: Lake Peipsi, zooplankton to phytoplankton biomass ratio, trophic state.

INTRODUCTION

Research of large lakes is highly complex as such lakes expand over a large area and are affected by an enormous number of different climatic and environmental factors (Blenckner, 2008). Various specific indicators and indexes are needed to facilitate the understanding of the state (and its changes) of large lakes. The zooplankton : phytoplankton biomass ratio (B_{Zp}/B_{Phyt}) largely reflects the type (effectiveness) of the food web in a water body and hence the nature of the ecosystem. Indirectly, it characterizes dominating groups in phyto- and zooplankton, feeding relationships between them and fish, as well as the pressure of fish on zooplankton. The B_{Zp}/B_{Phyt} ratio can be used as a marker criterion for the evaluation of the trophy of a water body and its ecosystem and, particularly, for permanent monitoring of a water body. This ratio decreases with the rise of the trophic state (Gulati, 1983; Andronikova, 1996; Jeppesen et al., 1999, 2000, 2005; Haberman & Laugaste, 2003). It is widely recognized that phytoplankton is influenced most by nutrients (bottom up) while zooplankton is influenced both by consumers (top down) and algae (bottom up). This causes their different seasonal dynamics and complicated relevant ratios. Thus, the values of the B_{Zp}/B_{Phyt} ratio are fluctuating within and across years. This variability has not been thoroughly analysed. Some data concerning this ratio for L. Peipsi have been published on the basis of plankton sampled up to the end of the last century (Haberman, 1996; Haberman & Laugaste, 2003; Nõges & Nõges, 2006). As the situation in the lake has changed markedly during this decade, a new analysis of the ratio has been initiated. About two decades ago, the ecosystem of the lake was in a quite good balance, and an effective algal food web prevailed in the open water (Nõges et al., 1993). Since the late 1990s and during the 2000s, the ecosystem of the lake lost its stability. The proportion of cyanobacteria in the biomass of summer phytoplankton increased consistently: from 20% to 70% in L. Peipsi *sensu stricto* (*s.s.*), and from 30% to 90% in the southern lake parts (Laugaste et al., 2007). An appreciable concentration of microcystins was detected in the lake water in the summer months of the 2000s (Tanner et al., 2005), and the biomass of the genus *Microcystis* exceeded 20 g m^{-3} in the southern lake parts in some years. At the same time, a continuous decline in zooplankton (Haberman et al., 2008) and changes in fish population (Kangur et al., 2008) were observed. The stock of planktivorous smelt (*Osmerus eperlanus eperlanus* m. *spirinchus* Pallas) and vendace (*Coregonus albula* (L.)) decreased drastically, and the abundance of piscivorous pikeperch (*Stizostedion lucioperca* (L.)) increased but, owing to overfishing, the amount of pikeperch is modest (Kangur et al., 2008). Nõges et al. (2005) explained the destabilization of the ecosystem with a decrease in the N : P ratio caused by increased phosphorus loading and reduced nitrogen loading in recent decades.

The aim of this study was to follow the variations of the B_{Zp}/B_{Phyt} ratio in different months, in different parts of the lake, and in different years; to establish boundaries of this variability, and to analyse how its changes reflect the state of the lake. We argue that the B_{Zp}/B_{Phyt} ratio (particularly the mean for a growing season) can be used as a marker characteristic for estimating the trophy of a water body.

STUDY SITE

Lake Peipsi *sensu lato* (*s.l.*) is a large (area 3555 km^2, the fourth largest lake in Europe) and shallow (mean depth 7.1 m), mainly unstratified lowland water body. Located on the Estonian–Russian border, L. Peipsi is the largest transboundary lake in Europe. Its volume of water is 25 m^3 at the long-term mean water level and the mean residence time is about two years. Water level fluctuations in the lake are considerable with an average annual range of 1.15 m (Jaani et al., 2008). The mostly agricultural catchment area of 47 800 km^2 is shared between Estonia (34%), Russia (58%), and Latvia (8%). The largest inflows are the Velikaya River in Russia and the Emajõgi River in Estonia. The Narva River, the only outflow from L. Peipsi, flows into the Gulf of Finland. It should be noted that the town of Narva (about 66 000 inhabitants) draws drinking water from this river. In the 1960s, the lake was covered by ice for up to 6 months, but in recent decades the ice-cover period has shortened up to 3–4 months; in winter 2008 no permanent ice-cover was formed. The water is the warmest (21–22 °C in open water) in July–August. The water is alkaline, the mean pH in the ice-free period is 8.36 (Milius & Haldna, 2008).

The lake consists of three different parts (Fig. 1). The northern part, the largest and deepest, is L. Peipsi *s.s.*, the southernmost part is L. Pihkva, which is connected with L. Peipsi *s.s.* by the narrow L. Lämmijärv. On the basis of the OECD (1982) classification, L. Peipsi *s.s.* is considered to be a eutrophic water body, while L. Pihkva is hypertrophic at present (Table 1). In the 1960s, L. Peipsi *s.s.* was almost mesotrophic and L. Pihkva was eutrophic (Starast et al., 2001). As a result of the decline in agricultural production in the catchment of L. Peipsi, the nutrient load to the lake decreased after the heavy loading in the 1980s (Nõges et al., 2005), but it increased again in the second half of the 1990s and in the 2000s. A continuous and even accelerating deterioration of the quality of the lake water has taken place up to the present (Milius & Haldna, 2008).

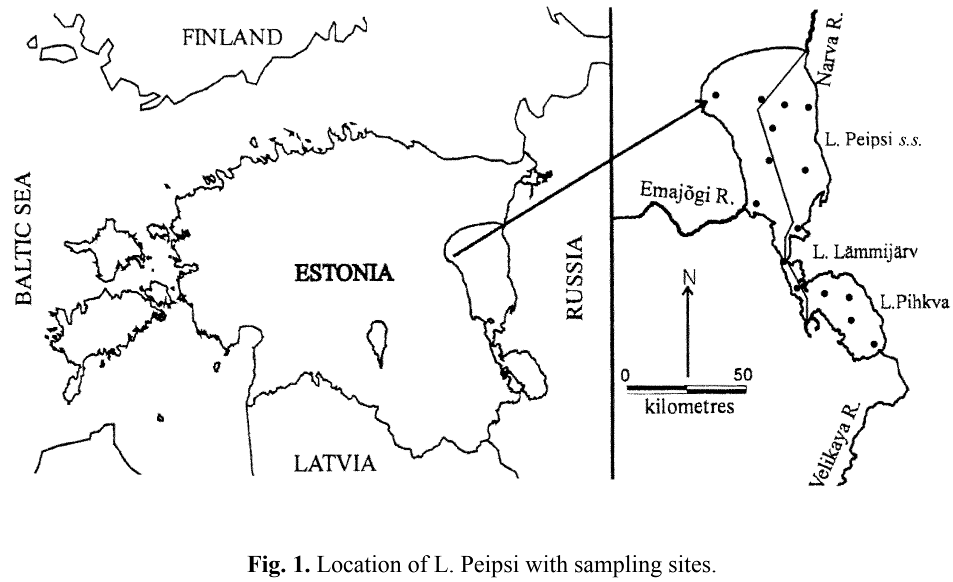

Fig. 1. Location of L. Peipsi with sampling sites.

Table 1. Comparison of lake parts: August 2003–2008

	L. Peipsi *s.s.*			L. Lämmijärv			L. Pihkva		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
TN, mg m^{-3}	637	410	1200	1114	640	1800	1189	930	1700
TP, mg m^{-3}	49	21	100	102	52	180	130	54	230
N : P	13	6	27	11	7	29	9	6	24
Chl *a*, mg m^{-3}	23	8	64	53	23	88	58	33	91
Secchi depth, m	1.5	0.8	2.2	0.8	0.5	2.0	0.6	0.4	0.7

MATERIALS AND METHODS

The material (hydrobiological and hydrochemical samples) was collected monthly (May–November) in 1997–2008; data for March were available in 1999 and 2002–2008, and for November in 1997–2003. Depending on the possibility of gathering samples also from the Russian side of the lake, the number of sampling sites varied from 6 to 15. The data for L. Pihkva (located almost entirely in Russia) were available only for March and August 2003–2008 and for October 2002. Integrated phyto- and zooplankton samples were taken from the whole water column of the pelagial zone of L. Peipsi *s.l.* The samples were collected with a Van Dorn sampler at 1 m depth intervals and mixed in the sampler tank. For zooplankton samples, 20 L of this mixed water was filtrated through a net of a 48 μm mesh. Both phyto- and zooplankton samples were preserved in Lugol's (acidified iodine) solution. The biovolume of phytoplankton was measured using the Utermöhl (1958) technique. The zooplankton samples were studied by conventional quantitative methods (Kiselev, 1956). The methods of collecting and treating samples are described in detail in Laugaste et al. (2001) and in Haberman (2001). Samples for nutrients and phyto- and zooplankton were taken and water parameters were measured simultaneously. Chemical determinations (total nitrogen (TN), dissolved inorganic nitrogen (DIN), total phosphorus (TP), and phosphate phosphorus (PO_4P)) were made by Tartu Environmental Research Ltd, Estonia. The Estonian Accreditation Centre hereby certifies that Tartu Environmental Research Laboratory has competence according to EN ISO/IEC 17025:2005 in the field of water, sediment, and soil chemical analysis. Flow analysis CFA and spectrometric detection were used. Statistical conclusions and tests were made using the statistical analysis package SAS/STAT procedure MIXED (SAS Institute, 1999). Our statistical model took into consideration the year-to-year and seasonal effects and their interaction as well as the fact that data from different parts of the lake may have different dispersions. Using the CONTRAST statement, we estimated differences in B_{Zp}/B_{Phyt} between two lake parts. The estimated standard deviation (SD) of the ratio was transformed back to the original scale, which showed how many times the ratio varied in relation to its mean value.

RESULTS

Although both zooplankton and phytoplankton are temperature dependent, the total biomass of either group has a different seasonal course in L. Peipsi *s.l.* Zooplankton follows more or less the course of water temperature with a peak in the summer months, while the dynamics of phytoplankton is more fluctuating with two or three peaks in the growing season and with the highest biomass frequently in autumn (Fig. 2). The spring and autumn peaks of phytoplankton commonly consist of diatoms, mainly *Aulacoseira islandica* (O. Müller) Sim., the summer peak is comprised of cyanobacteria (alternately the genera *Gloeotrichia*, *Anabaena*, *Aphanizomenon*, and *Microcystis*). In some years, cyanobacteria (mainly *Aphanizomenon*) play quite an important role in the autumn biomass, as do diatoms (*Aulacoseira ambigua* (O. Müller) Sim., *Stephanodiscus* spp. etc.) in summer biomass. In March and April, zooplankton abundance was dominated (20% or more of both abundance and biomass) by the thermophobic rotifers *Polyarthra dolichoptera* Idelson and *Synchaeta verrucosa* Nipkow, and their biomass was dominated by juvenile forms of the genus *Mesocyclops* and *Cyclops kolensis* Lilljeborg. In spring (May) rotifers and copepod juveniles continued to dominate, but the share of filter-feeding copepodites in the zooplankton biomass increased significantly. In summer and autumn, the same species of the genera *Daphnia*, *Bosmina*, and *Eudiaptomus gracilis* (Sars) were commonly dominating, but their biomass was different. In early summer (June) and in late summer (September) the role of the genus *Bosmina* and copepods in the zooplankton biomass was greater than in July when cladocerans, particularly *Daphnia cucullata* Sars, were prevalent.

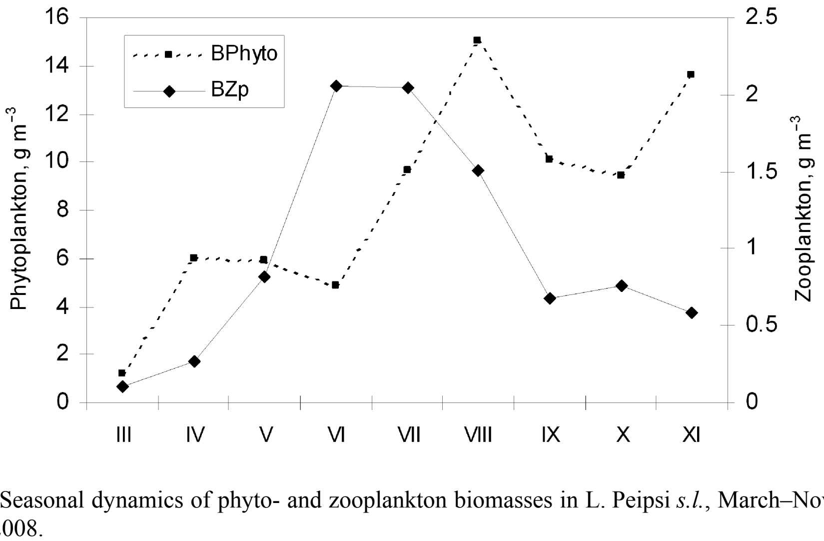

Fig. 2. Seasonal dynamics of phyto- and zooplankton biomasses in L. Peipsi *s.l.*, March–November 1997–2008.

The B_{Zp}/B_{Phyt} ratio revealed clear differences between the moderately eutrophic northern part, L. Peipsi *s.s.*, and the hypertrophic southern parts, L. Lämmijärv and L. Pihkva (Fig. 3). For comparison of three lake parts, only data for March, August, and October (only one year) were available. A clear difference according to the trophic state was apparent. The ratio was highest for the northern part of the lake (mean values for August declined from north to south: 0.18, 0.07, and 0.06, Fig. 4). A conformity of B_{Zp}/B_{Phyt} with the trophic state is proved by its relationship with Secchi disc values (Fig. 5).

The B_{Zp}/B_{Phyt} values fluctuated during the vegetation period (Fig. 3), increasing already in May, peaking in June (clear-water period), and decreasing sharply in the summer months, with an annual minimum in late autumn (Table 2). During 1997–2008 the average values of B_{Zp}/B_{Phyt} for the growing season were lower than 0.5, being 0.27 for L. Peipsi *s.s.* and 0.16 for L. Lämmijärv. The monthly values of B_{Zp}/B_{Phyt} fluctuated in a wide range: from 0.06 to 0.62 for L. Peipsi *s.s.* and L. Lämmijärv. For L. Pihkva, this value was available only for March (0.004), August (0.06), and October (0.08). Maximum values (up to 2) occurred for L. Peipsi *s.s.* in June and quite an essential increase in this value (up to 1) was also found in May. In parallel with the increasing trophic state of the lake, the mean values of B_{Zp}/B_{Phyt} for the growing season decreased from 0.50 at the beginning of the 1990s (Haberman & Laugaste, 2003) to 0.18 in 2008.

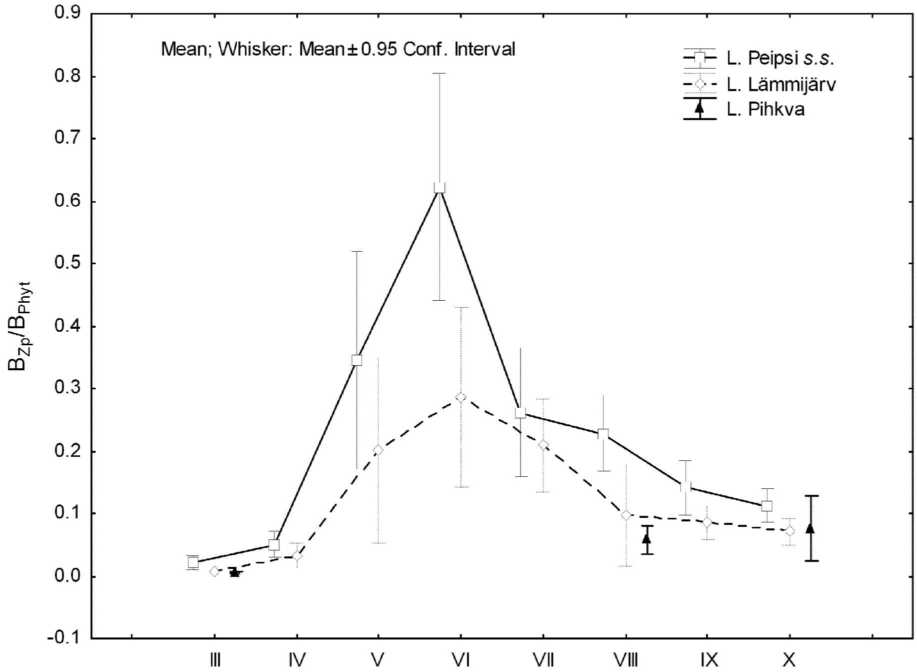

Fig. 3. Seasonal dynamics of the zooplankton : phytoplankton biomass ratio (B_{Zp}/B_{Phyt}) for different parts of L. Peipsi, 1997–2008.

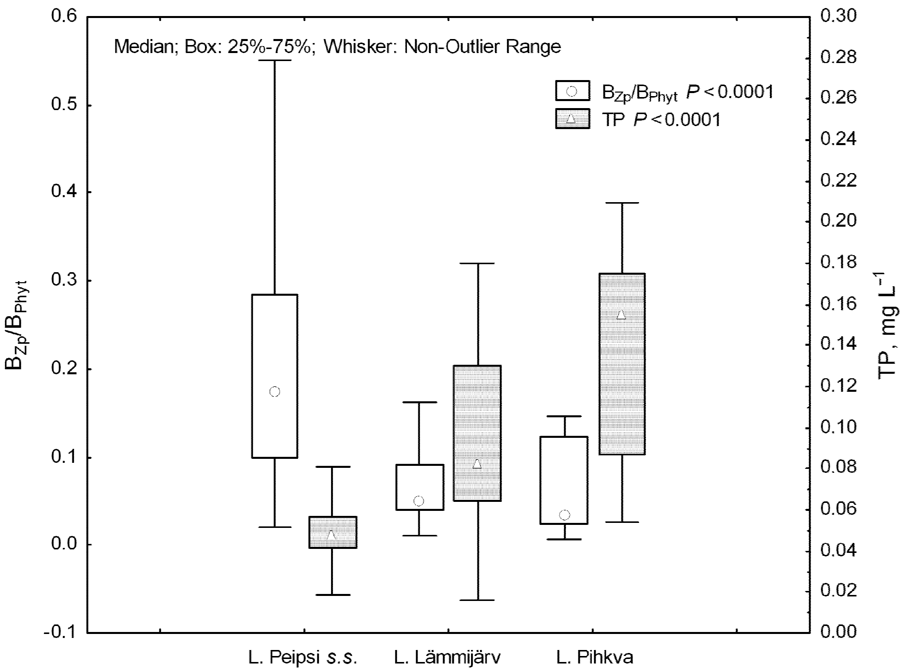

Fig. 4. Differences of B_{Zp}/B_{Phyt} and TP in lake parts in August, mean values for 2003–2008. *P*-value indicates significance of differences between L. Peipsi *s.s.* and L. Lämmijärv.

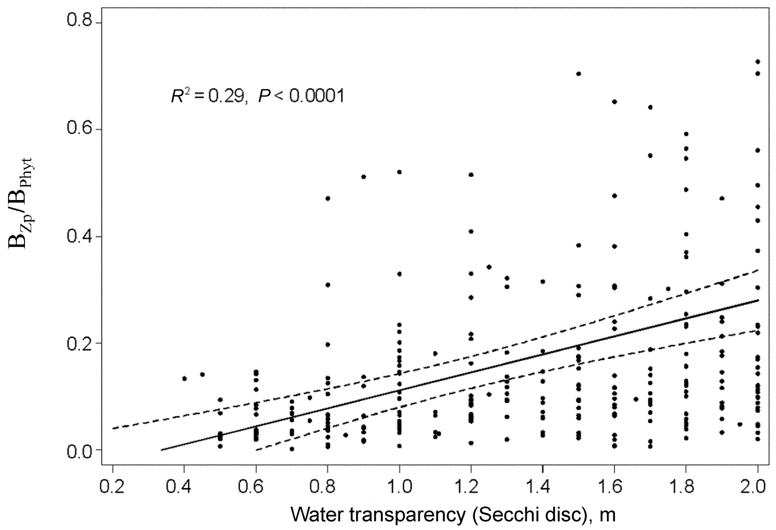

Fig. 5. Relationships between B_{Zp}/B_{Phyt} and Secchi disc depths in summer, all lake parts in 1997–2008.

Table 2. Zooplankton:phytoplankton biomass ratio for L. Peipsi *s.s.* and L. Lämmijärv, descriptive statistics in different months, means for 1997–2008. Quality class was estimated on the basis of Nõges & Nõges (2006)

Month	Lake part	Valid N	Mean ± SE	Var. coeff.	25%ile	75%ile	Quality class
III	Peipsi *s.s.*	37	0.02 ± 0.005	1.47	0.004	0.028	?
	Lämmijärv	14	0.01 ± 0.002	0.75	0.005	0.013	
IV	Peipsi *s.s.*	25	0.05 ± 0.011	1.04	0.008	0.083	Moderate
	Lämmijärv	10	0.03 ± 0.009	0.84	0.015	0.059	Poor
V	Peipsi *s.s.*	28	0.35 ± 0.085	1.30	0.038	0.500	Moderate
	Lämmijärv	17	0.20 ± 0.070	1.45	0.051	0.217	Moderate
VI	Peipsi *s.s.*	28	0.62 ± 0.088	0.75	0.233	0.922	Good
	Lämmijärv	17	0.29 ± 0.069	0.98	0.135	0.288	Moderate
VII	Peipsi *s.s.*	28	0.26 ± 0.050	1.02	0.097	0.389	Moderate
	Lämmijärv	17	0.21 ± 0.035	0.68	0.095	0.320	Moderate
VIII	Peipsi *s.s.*	51	0.23 ± 0.030	0.93	0.095	0.248	Moderate
	Lämmijärv	23	0.10 ± 0.039	1.92	0.029	0.084	Moderate/poor
IX	Peipsi *s.s.*	29	0.14 ± 0.022	0.83	0.084	0.143	Moderate
	Lämmijärv	17	0.08 ± 0.012	0.59	0.054	0.121	Moderate
X	Peipsi *s.s.*	61	0.13 ± 0.012	0.78	0.077	0.139	Moderate
	Lämmijärv	34	0.08 ± 0.008	0.59	0.043	0.089	Moderate/poor
XI*	Peipsi *s.s.*	22	0.06 ± 0.007	0.61	0.022	0.078	Moderate
	Lämmijärv	8	0.06 ± 0.019	0.55	0.028	0.094	Moderate
V–X	Peipsi *s.s.*	196	0.27 ± 0.023	1.20	0.088	0.305	Moderate
	Lämmijärv	108	0.16 ± 0.020	1.31	0.045	0.164	Moderate

* Data available up to 2003.

According to the standard deviation of the log-transformed values, variation of the B_{Zp}/B_{Phyt} ratio in relation to its mean value for the growing season was 3.22. The ratio varied most in May (Fig. 6); this is explicable with differences in the melting time of the ice cover and therefore, in the timing of the spring peak of phytoplankton. The coefficient of variation shows quite a wide range of variation also in August (Table 2). This means that in these months the absolute values of phytoplankton (water bloom caused by cyanobacteria) differed by years and depended most on weather conditions. The ratio showed lowest variation in autumn months.

Analysis of the dynamics of B_{Zp}/B_{Phyt} over the last 12 years revealed a sharp decrease in its values since 2000 (Fig. 7). In parallel with the increasing trophic state of the lake, the mean values of B_{Zp}/B_{Phyt} for the growing season decreased from 0.34 in 1997 to 0.18 in 2008 in L. Peipsi *s.s.* and from 0.24 to 0.10 in L. Lämmijärv. Beginning from 1997, the mean values of the ratio decreased from 0.24 to 0.16 in L. Peipsi *s.s.*, and from 0.18 to 0.06 in the southern lake parts in the summer months (Fig. 8).

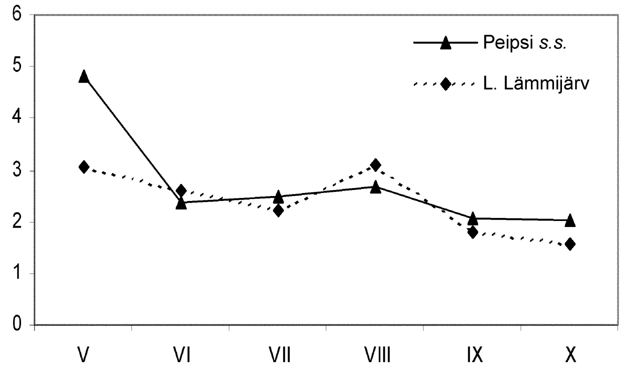

Fig. 6. Variability of B_{Zp}/B_{Phyt}, mean for the growing seasons of 1997–2008. The *y*-axis shows how many times the ratio varies in relation to its mean (see Methods).

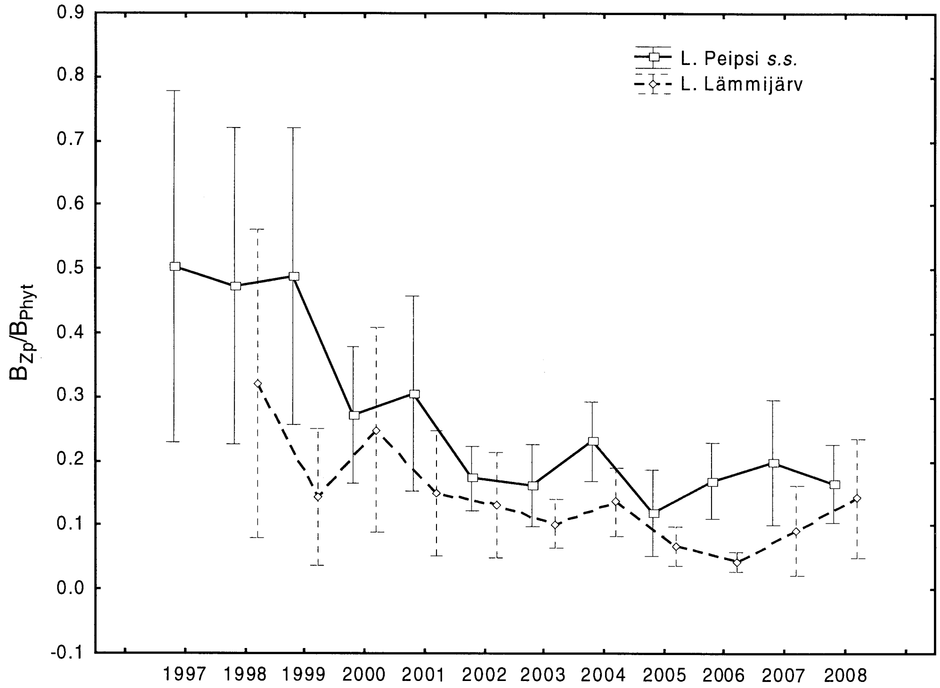

Fig. 7. Dynamics of the B_{Zp}/B_{Phyt} ratio by years, mean values of May–October for lakes Peipsi *s.s.* and Lämmijärv.

It is worth stressing that the B_{Zp}/B_{Phyt} ratio had only weak significant negative correlations with nutrients (TN, TP, and mineral forms of N and P) for the whole lake; however, stronger correlations with TP were observed in L. Peipsi *s.s.* (Fig. 9). Clear differences in the B_{Zp}/B_{Phyt} ratio and in the phosphorus concen-

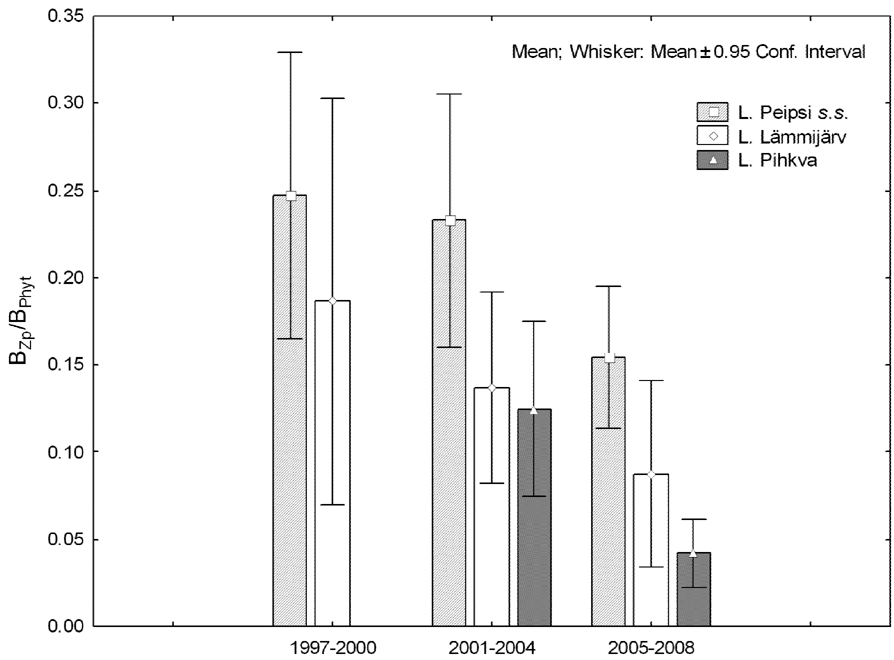

Fig. 8. Dynamics of the B_{Zp}/B_{Phyt} ratio in the lake parts, mean values for August in 1997–2008.

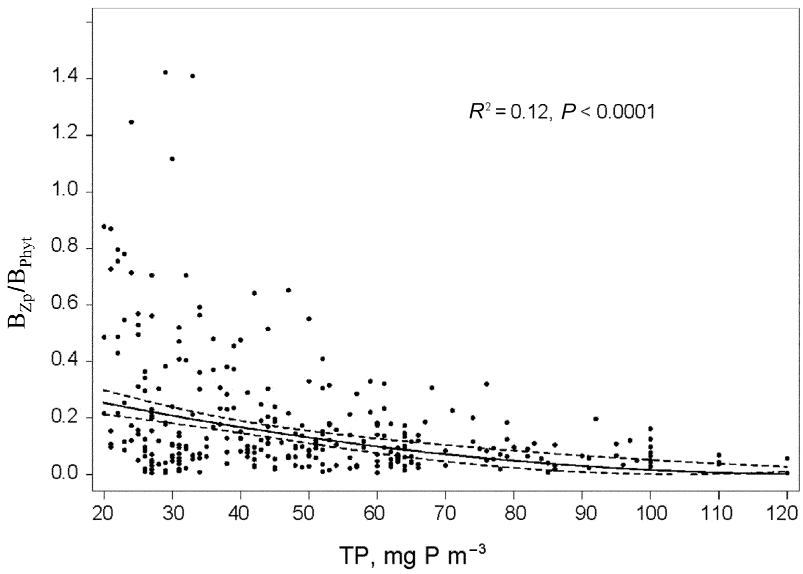

Fig. 9. Relationships between B_{Zp}/B_{Phyt} and TP in L. Peipsi *s.s.*, mean values for 1997–2008.

tration were established between the northern and southern lake parts (Fig. 4). The associations of B_{Zp}/B_{Phyt} with nutrients were analysed separately for each month. Correlations with TP were revealed for June ($r = -0.46$, $P < 0.0001$), August ($r = -0.28$, $P < 0.002$), and October ($r = -0.35$, $P < 0.001$).

DISCUSSION

Long-term investigations have demonstrated that the water characteristics and biological communities in L. Peipsi differ between the northern to southern parts of the lake (Haberman et al., 2008; Kangur & Möls, 2008). The northern and deepest part (mean depth 8.3 m), L. Peipsi *s.s.*, is significantly less loaded with nutrients and is more transparent (2.5 times) than the southern very shallow (mean depth 3.8 m) L. Pihkva. The discrepancy of the phosphorus content and N : P ratio between the northern and southern lake parts has increased: in the southern lake parts the TP content has increased while the N : P ratio has decreased (Kangur & Möls, 2008). Also, a decrease in the B_{Zp}/B_{Phyt} ratio towards higher trophy is evident (Figs 4 and 9). In August (mean for 2003–2008) this ratio was 0.23 in L. Peipsi *s.s.* (TP 49 μg L^{-1}), 0.10 in L. Lämmijärv (TP 102 μg L^{-1}), and 0.06 in L. Pihkva (TP 130 μg L^{-1}). In the 2000s, the TP content reached 230 μg L^{-1} in L. Pihkva. In oligo-mesotrophic Dutch lakes, B_{Zp}/B_{Phyt} fluctuates between 0.45 and 0.78, while in eutrophic lakes it ranges from 0.13 to 0.32 (Jeppesen et al., 1999). A study of Danish lakes of different trophy showed that a rise in the trophic state (TP content <0.05 to 0.4 mg L^{-1}) is accompanied by a decrease in the B_{Zp}/B_{Phyt} ratio from 0.46 to 0.08 (Jeppesen et al., 2000). Later, Jeppesen et al. (2005) found that this ratio is generally low for TP concentrations >100 μg L^{-1} but increases in many lakes below this threshold. In the strongly eutrophic L. Võrtsjärv (Estonia) this ratio ranges from 0.06 to 0.22 during the vegetation period, with an average of 0.13 (Haberman, 1998). The B_{Zp}/B_{Phyt} ratios in other European lakes with lower trophy are the following: in the oligo-mesotrophic L. Onega 0.7–1.1 (calculated by Kaufman, 1990); in the meso-oligotrophic L. Ladoga 0.5–0.7 (calculated by Rumyantsev & Drabkova, 2002); in the oligo-mesotrophic L. Saimaa 0.6 (Hynynen et al., 1999); in the oligo-mesotrophic L. Vänern (lake part Tärnan) 1.3 for August 1976–2007 (Sonesten, 2008).

The seasonal variability of the B_{Zp}/B_{Phyt} ratio is caused by different courses of both plankton groups during the growing season (Fig. 2): the highest ratio in June reflects a drop in phytoplankton biomass, which is related to the end of the early spring peak with alternating dominants and the increasing grazing of zooplankton. The mean ratio 0.62 in June allows us to suppose that in June the efficient algal food chain may occur while in the other months the inefficient microbial food chain may be prevalent (Table 2). It is worth noting that small-celled algae and large-bodied zooplankters (gen. *Bosmina* and *Daphnia*) are prevailing in June. Generally, a decrease in the B_{Zp}/B_{Phyt} ratio in summer may indicate increasing fish predation and decreasing grazing by filter-feeding zooplankton. It is known that the role of fish in the formation of the mean B_{Zp}/B_{Phyt} is significant

(Jeppesen et al., 2002, 2005; Iglesias et al., 2008; Amundsen et al., 2009). In L. Peipsi, the impact of fish on the zooplankton community was important in the 1960s when the fish community was dominated by planktivorous vendace and smelt (Ibneeva & Dorozhkina, 1983). At the present time, vendace and smelt have almost disappared from the fish community of L. Peipsi (Kangur et al., 2008). The effect of pikeperch and perch (*Perca fluviatilis* L.) juveniles on zooplankton may be essential but it does not offset the possible effect of almost vanished smelt and vendace. Not ignoring the influence of planktivorous fishes, we are of the opinion that the supreme factor causing the drop in the summer B_{Zp}/B_{Phyt} is the high biomass of phytoplankton with dominating toxic cyanobacteria rather than fish predation. In the 1980s and 1990s, the percentage of filter-feeding zooplankton production in primary production was quite high (6.2–10%). It was assumed that the direct relationship between zoo- and phytoplankton in the four-link food chain (phytoplankton – herbivorous zooplankton – planktivorous fishes – piscivorous fishes) was prevalent and the role of the microbial food chain was modest in L. Peipsi *s.s.* Consequently, phytoplankton was controlled by top-down (zooplankton) forces, and up to 20% of phytoplankton production was consumed by zooplankton (Nõges et al., 1993, 2001; Haberman, 2001). Under the heavy nitrogen loading in the 1980s, no extensive cyanobacterial blooms were observed, but these started again in the 1990s with the decreasing TN : TP ratio from 38 to 13 in L. Peipsi *s.s.* This favoured development of cyanobacteria, including N_2-fixing species; and the critical value of the TN : TP mass ratio for cyanobacteria in L. Peipsi is 30 (Nõges et al., 2008), which is far higher than the ratio for summer in the 2000s (Table 1). This is reflected in the B_{Zp}/B_{Phyt} ratio: its mean value in the 1980s was 0.70 for the growing season (May–October) in L. Peipsi *s.s.*, which indicates the boundary between meso- and eutrophy (Haberman, 1996). Milius & Haldna (2008) stressed that a clear rise in the trophic state of L. Peipsi occurred in the late 1990s and in the 2000s compared with the 1980s. In L. Pihkva the TP content increased 2.4 times during this period. According to Downing et al. (2001), the proportion of cyanobacteria forms an average of 60% of phytoplankton biomass at TP above 80–90 µg L^{-1}. It is well known that phytoplankton serves as an early risk indicator owing to its rapid response to changes in the environment, primary role in the food web, and influence on other organisms, as well as a good indicator of changes in water quality (Willén, 2001). Since 1997 the share of cyanobacteria in phytoplankton biomass has increased up to 90% in the southern parts of the lake in summer. In parallel with increasing cyanobacterial blooms, a marked decline occurred in zooplankton (Laugaste et al., 2007). In 1985–1996, the mean zooplankton biomass in summer (July–August) was about 3 g m^{-3} (Haberman, 2001), while starting from the early 2000s it diminished to about 1 g m^{-3}. The decreasing trend characterizes all zooplankton groups: rotifers, cladocerans, copepods, and veligers of *Dreissena polymorpha* Pallas. According to Tanner et al. (2005), the concentration of microcystins (5 types) in the open area of L. Peipsi *s.s.* at a depth of 30–50 cm is maximally 50 µg L^{-1}. Compared with literature data (Watanabe et al., 2000; Lindholm et al., 2003), the concentration of toxins in L. Peipsi appears to be very high in some cases, which definitely affects the biota. Several studies indicate to harmful effects of toxins and bloom extracts on zooplankton (Gilbert, 1990, 1994; Ghadouani et al., 2003; Barreiro et al., 2007). Beginning from 1997, the mean values of the B_{Zp}/B_{Phyt} ratio in L. Peipsi decreased significantly in summer months (Fig. 8), which clearly reflects the worsening of the trophic state and water quality. Likewise, in the mesotrophic Lake Krasnoye in Russia, the B_{Zp}/B_{Phyt} ratio changed in parallel with increasing trophy from 0.62 in the 1960s to 0.21 in the late 1990s (Trifonova & Makartseva, 2003). A low B_{Zp}/B_{Phyt} ratio suggests that the impact of herbivory (top-down pressure on phytoplankton) is unimportant and the bulk of primary production remains uneaten (Gulati, 1983; Haberman, 1998; Scharf, 1999), which is likely for L. Peipsi *s.s.* and apparent for L. Pihkva. Jeppesen et al. (1999) claim that the grazing pressure on phytoplankton is strong in mesotrophic lakes and weak in eutrophic waters. Jeppesen et al. (2000) found that herbivorous zooplankton consumes 50% of algal biomass per day in lakes of low trophy (<0.05 mg P L^{-1}) but 16–19% at the trophic state 0.2–0.4 mg P L^{-1}.

The zooplankton to phytoplankton biomass ratio reflects differences between the lake parts quite vividly (Fig. 4). Nõges & Nõges (2006) set the boundaries of quality classes for the B_{Zp}/B_{Phyt} ratio for L. Peipsi *s.l.* To avoid seasonally fluctuating values in estimation, they split long-term data into monthly subsets and applied a percentile-based approach to set the class boundaries. The principle was that at least half of the values for every month (25th to 75th percentiles) must fit some quality class. The data set for 1982–2002 analysed by Nõges & Nõges (2006) reflected the state of the ecosystem before the decline in the amount of zooplankton in the 2000s. Our monthly values of B_{Zp}/B_{Phyt} for 1997–2008 coincide with their assessment and, consequently, L. Peipsi belongs to the class of lakes of moderate quality (Table 2). Nõges & Nõges (2006) did not set boundaries for March, July, and August, for which the values did not correlate with total phosphorus. Our opinion is that the B_{Zp}/B_{Phyt} ratio for the summer months is informative; however, to avoid the situation where the ratio will depend mainly on the timing of the cyanobacterial bloom (depending on weather conditions, the ratio can vary tens of times), the mean values for the vegetation period are more suitable to estimate the state of a lake as in this case monthly fluctuations will be smoothed.

The B_{Zp}/B_{Phyt} values for March do not fit any definite quality class. The low values for October and November (Table 2) do not indicate a clear degradation of the ecosystem in autumn but reflect the longer growing season of phytoplankton compared to zooplankton. Still, it is worth mentioning that the continuously growing role of the small-bodied indicator of eutrophy *Chydorus sphaericus* Müller (Gulati, 1983; Haberman, 1998; Haberman & Laugaste, 2003) reduces zooplankton biomass in autumn. Quality class is not tantamount to trophic state. However, the mean values of B_{Zp}/B_{Phyt} for the vegetation period for L. Peipsi (Table 2) fall into the boundaries of the eutrophic state according to numerous literature data. Andronikova (1996) stated that the B_{Zp}/B_{Phyt} ratio is about 4.32 ± 1.20 for oligotrophic, 0.78 ± 0.14 for mesotrophic, and 0.42 ± 0.07 for eutrophic water bodies. In the Netherlands, this ratio is 0.4 for oligo-mesotrophic lakes and 0.05 for hypertrophic lakes (Gulati, 1983). For the Estonian hypertrophic Lake Petajärv this ratio is 0.01 in summer, for the Belarusian hypertrophic Lake Dauble 0.04, and for the Estonian oligotrophic Lake Nohipalu Valgjärv 2–3 (Laugaste & Pork, 1980). For Lake Pyhäjärvi in Finland with a low trophy (TP in summer 15 μg L^{-1}) this ratio is 2–5 (Sarvala et al., 1984). It is evident that the mean values of B_{Zp}/B_{Phyt} for L. Peipsi *s.l.* did not achieve mesotrophic level according to Andronikova (1996) even at the time of its maxima in June; however, more than 25% of the values attained this level (Table 2). Comparison of the values of B_{Zp}/B_{Phyt} to those of other water bodies suggests that the state of L. Peipsi *s.s.* is eutrophic, while that of L. Pihkva is hypertrophic.

In conclusion, our data reveal quite considerable fluctuations in the B_{Zp}/B_{Phyt} ratio during the growing season with maxima in June (clear-water period) and minima in October–November. The mean values and 25th and 75th percentiles of the B_{Zp}/B_{Phyt} ratio indicate the class of moderate quality, as well as the eutrophic state of L. Peipsi *s.s.* and the hypertrophic state of L. Pihkva and L. Lämmijärv. Its average values for the growing season will smooth monthly fluctuations and reveal statistically significant differences between the parts of the lake with different levels of trophy. Our results confirm that the mean values of the B_{Zp}/B_{Phyt} ratio for the growing season can be used as marker criteria in the evaluation of the trophy of a water body and its ecosystem, particularly that of large lakes.

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Zoo- ja fütoplanktoni suhte ajaline ning ruumiline muutlikkus suures madalas järves

Kätlin Blank, Reet Laugaste ja Juta Haberman

Suurte järvede uurimine on komplitseeritud, kuna järved laiuvad suurel alal ja on allutatud tohutule hulgale erinevatele mõjuritele. Selliste järvede uurimise hõlbustamiseks on igasugused asjakohased suhted ja indeksid teretulnud. Peipsi järv on Euroopas suuruselt (3555 km^2) neljas, olles piirijärv Eesti ja Venemaa vahel. Vastavalt OECD (1982) klassifikatsioonile on Peipsi põhjapoolsem, sügavam osa – Peipsi Suurjärv e Peipsi *sensu stricto* – eutroofne, lõunapoolne osa – Pihkva järv koos kaht osa ühendava Lämmijärvega – aga hüpertroofne. Antud töö eesmärgiks oli uurida Peipsis zoo- ja fütoplanktoni biomasside suhet (B_{Zp}/B_{Phyt}) nii ajas (aastail 1997–2008 ning eri kuudel) kui ruumis (järve eri osades) ja välja selgitada selle suhte väärtus järve seisundi hindamisel. Järve troofsustase suureneb ja B_{Zp}/B_{Phyt} väheneb suunal põhjast lõunasse (tabel 1, joonis 4). Augustis aastail 2003–2008 oli see suhe Suurjärves 0,18, Lämmijärves 0,07 ja Pihkva järves 0,06.

B_{Zp}/B_{Phyt} kõigub sesoonselt suurtes piirides (tabel 2), saavutades maksimumi juunis ja miinimumi oktoobris-novembris. Juunis on planktonis suhteliselt palju zooplanktonile toiduks sobivaid ainurakseid vetikaid ja vähe neile sobimatuid sinivetikaid; samal ajal on tõusmas soojalembeste vetikatoiduliste zooplankterite (eelkõige *Daphnia* ning *Bosmina* liikide) arv. Suhte suur keskmine väärtus juunis Peipsis *s.s.* (0,62) peegeldab järve ökosüsteemi suhteliselt head seisundit. Zooplankton toitub vetikatest ja järves on valdav efektiivne toiduahel. Teistel kuudel on ülekaalus väheefektiivne mikroobiringe. Alates 1997. aastast on vegetatsiooniperioodi keskmine B_{Zp}/B_{Phyt} langenud Suurjärves 0,34-lt 0,18-le ja järve lõunaosades 0,24-lt 0,10-le. See näitab järve troofsuse suurenemist ja veekvaliteedi halvenemist.

Kuude lõikes on indeksi varieeruvus suurim mais ja augustis ning väikseim oktoobris-novembris (tabel 2, joonis 6). Peipsi troofsustaseme hindamiseks on otstarbekas kasutada vegetatsiooniperioodi (maist oktoobrini) keskmist indeksi väärtust, mis silub indeksi varieeruvuse sesooniti.