



The ecological state of Lake Peipsi (Estonia/Russia): improvement, stabilization or deterioration?

Kätlin Blank^{a*}, Enn Loigu^b, Reet Laugaste^a, and Juta Haberman^a

^a Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 61101 Rannu, Estonia

^b Department of Environmental Engineering, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia

Received 15 February 2016, revised 13 May 2016, accepted 7 June 2016, available online 29 December 2016

© 2016 Authors. This is an Open Access article distributed under the terms and conditions of the Creative Commons Attribution-NonCommercial 4.0 International License (<http://creativecommons.org/licenses/by-nc/4.0/>).

Abstract. Lake Peipsi *sensu lato* consists of limnologically and hydrochemically different parts, Lake Peipsi *sensu stricto*, Lake Lämmijärv, and Lake Pihkva. The eutrophic L. Peipsi *s.s.* and the hypertrophic Lake Pihkva were studied. The aim was to find out if the ecological state of these lake parts has improved, stabilized or deteriorated during a ten-year period, 2003–2012. For this purpose, data on loadings, in-lake nutrient concentrations, water transparency, water level, chlorophyll *a* concentration, as well as phyto- and zooplankton were compared for two five-year sub-periods (2003–2007 and 2008–2012). Comparison demonstrated a decline in the loading of total phosphorus (TP) from rivers on the Estonian and Russian sides as well as in its mean concentration in both lake parts. Both phytoplankton biomass and cyanobacterial biomass decreased in response to the reduced nutrient content in the lake water. The responses of zooplankton were contradictory. Changes in the occurrence of indicator species and declining mean zooplankton weight reflected a continuous eutrophication process while changes in the abundance of rotifers and the genus *Daphnia* indicated a subtle shift towards recovery. Our results show a modest improvement in the ecological condition of both lake parts.

Key words: lake recovery, eutrophic lake, hypertrophic lake, pollution load, nutrients, plankton response.

INTRODUCTION

Most lakes throughout the world have been modified to some extent by human activity (Bennion et al., 2015). Serious water quality problems (eutrophication) commonly result in changes in phytoplankton productivity (algal blooms), pH fluctuations, dissolved oxygen and electrical conductivity levels, and a general decrease in aquatic biodiversity (Verschuren et al., 2002), which cause problems for humans through contaminated water supplies and for the ecological quality of lakes (Räike et al., 2003). In order to curb increasing eutrophication, the European Union compiled a Water Framework Directive (WFD, Directive 2000/60/EC) in 2000 (EU, 2000). The main

goals of this directive are to avoid further deterioration of water bodies as well as to protect and improve the condition of aquatic ecosystems and their directly dependent terrestrial ecosystems and wetlands with respect to their water supply (Glenk et al., 2011). As the good ecological state of water bodies could not be achieved by 2015, the European Commission extended the deadline until 2027 (European Commission, 2009).

Numerous efforts have been made to restore lakes; however, the results are not as good as expected. In spite of many individual success stories, there remains considerable uncertainty about whether restoration targets can be achieved and over what timescales one might expect to see improvement. Recovery may be a slow process as biotic communities tend to exhibit hysteresis and time lags, and thus ecosystems take time to re-

* Corresponding author, Katlin.Blank@emu.ee

adjust to reduced stress (e.g. Yan et al., 2003; Johnson and Angeler, 2010). Jeppesen et al. (2005) in their study of 35 lakes concluded that for most lakes, internal loading (especially phosphorus) evidently delays recovery by 5–10 years. Recovery of lakes after nutrient loading reduction may be confounded by concomitant environmental changes such as global warming. Dokulil and Teubner (2005) reported that in Mondsee, a eutrophicated alpine lake in Austria, annual mean phytoplankton biomass continued at first increasing after phosphorus concentration began to decline. The expected decrease in phytoplankton biomass was delayed by about 5 years. The underlying reason was that several phytoplankton species differed in the timing of their responses to changing nutrient conditions. A substantial delay in the response to the nutrient input decrease was found also for Loch Leven (Carvalho et al., 2012), where climate changes hindered restoration efforts. The clearest climate impact was the negative relationship between summer rainfall and chlorophyll *a* (Chl*a*) concentrations. Mao and Richards (2012) concluded that the decline in water quality may be irreversible because it is impossible to eliminate external stress to an appropriate degree.

A considerable effort has been made to reduce external nutrient loads to L. Peipsi. The largest point polluter from the Estonian side is the town of Tartu (about 98 000 inhabitants) on the banks of the Emajõgi River. Since 1998, 80% of the wastewater from Tartu has been purified chemically, the efficiency of nitrogen removal has been over 50% and phosphorus removal 85–90%. The largest polluter on the Russian side is the Velikaya River with the town of Pskov (about 206 000 inhabitants) but the sewage is purified only biologically without the extraction of phosphorus (Loigu et al., 2008).

In the 1960s, L. Peipsi *sensu stricto* (*s.s.*) was almost mesotrophic and L. Pihkva was eutrophic (Starast et al., 2001). Further, eutrophication of surface waters started from the 1970s. After the collapse of wasteful agriculture in the early 1990s, diffuse loading decreased sharply, by 53% and 44%, as regards N and P loading, respectively (Loigu and Leisk, 1996). However, in spite of the drop in the external loading, the P content in the southern part of the lake continued to increase in the 1990s. The ecological condition of L. Peipsi *s.s.* and especially that of L. Pihkva began to be characterized by massive potentially toxic cyanobacterial blooms, drastic nocturnal oxygen shortages, and fish kills (Haberman et al., 2010; Kangur et al., 2013).

The current study focused on the two contrasting lake parts with respect to morphology, external loadings, nutrient content, and water management legislation: eutrophic L. Peipsi *s.s.* and hypertrophic L. Pihkva. The aims were (1) to follow the response of the quality of lake water to changes in pollution loadings; (2) to analyse

how phytoplankton, the first to react, responds to changes in water nutrient concentration; (3) to find out the response of zooplankton metrics to reflect changes in hydrochemistry and phytoplankton during the period under study. We hypothesized that (1) after a decline in the nutrient loading from rivers, the ecological condition of the lake will display quite clear responses of phytoplankton (faster responder) but variable results for zooplankton; (2) a shallower water body (L. Pihkva) is more sensitive to changes in nutrient loadings than a deeper lake (L. Peipsi *s.s.*).

STUDY SITE

Lake Peipsi *sensu lato* (*s.l.*) with an area of 3555 km² is divided between two countries, Estonia (44%) and Russia (56%), being the largest transboundary lake in Europe. It consists of three limnologically and hydrochemically different parts (Fig. 1): L. Peipsi *s.s.* (area 2611 km², mean depth 8.3 m), L. Lämmijärv (236 km², 2.5 m), L. Pihkva (708 km², 3.8 m). The whole lake is well mixed by the wind and well aerated by the waves and currents; there is no permanent stratification of tem-

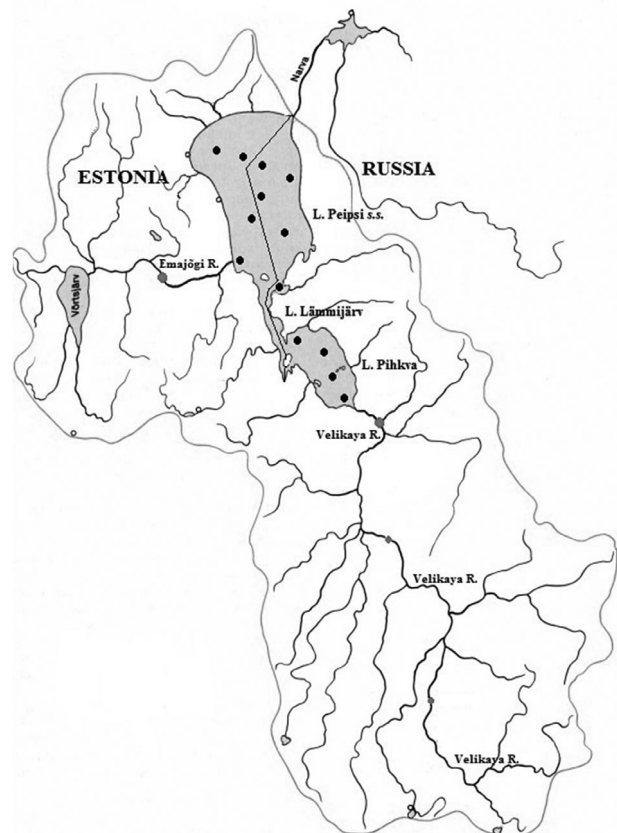


Fig. 1. Drainage basin of Lake Peipsi *s.l.* and location of the sampling points.

perature, oxygen content, or hydrochemical parameters in the ice-free period. The water is the warmest (21–22 °C in open water) in July–August.

MATERIAL AND METHODS

Hydrobiological and hydrochemical (in-lake water nutrients) samples were taken in August 2003–2012. Nine fixed sampling stations in the pelagial of L. Peipsi *s.s.* and four stations in L. Pihkva were sampled during each monitoring trip (Fig. 1). On the lake, a series of 2-litre samples was taken with a van Dorn sampler at 1 m intervals from the surface to a depth of approximately 0.5 m above the sediments. The 2-L samples were poured together into a tank to make a composite sample. Samples for phytoplankton and Chl*a* were taken directly from this tank filled with mixed water; for zooplankton, 20 L was filtered through a plankton net with a mesh size of 30 µm. Phyto- and zooplankton samples were preserved with Lugol's (acidified iodine) solution. Water transparency (Secchi depth, SD) was measured with a Secchi disc (diameter 30 cm). The methods of collecting and treating samples are described in detail in (Laugaste et al., 2001) and in (Haberman, 2001). Hydrochemical samples were analysed in the Tartu Branch of the Estonian Environmental Research Centre. The data from riverine pollution (2001–2011) were from the Department of Environmental Engineering, Tallinn University of Technology. The modelling approach to the determination of nutrient loads from rivers is described in detail in (Piirimäe et al., 2015).

The study period of 2003–2012 was divided into two sub-periods, 2003–2007 and 2008–2012, on the basis of the dynamics of total phosphorus (TP). In the second sub-period the concentration of TP attained a more stable state in both lake parts (especially in L. Peipsi *s.s.*) compared to the first sub-period (Fig. 2). This phenomenon

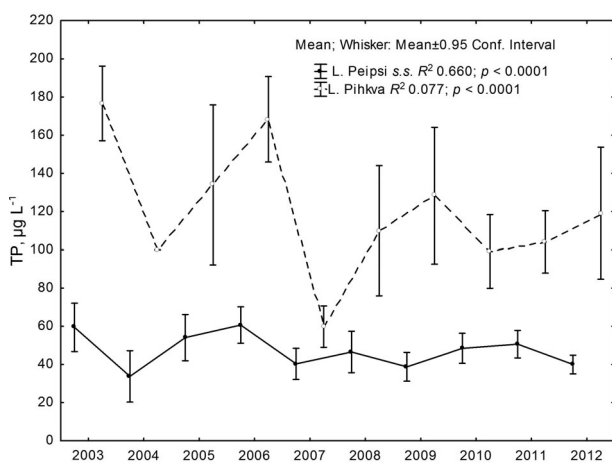


Fig. 2. Dynamics of total phosphorus (TP) in the water of L. Peipsi *s.s.* and L. Pihkva, data for August.

raises the question about the consequences for the ecosystem of the lake. To compare the mean values for the two sub-periods, the *t*-test was used. To explore long-term trends and the relationship between water level (WL) and plankton variables, a linear regression model was employed. The data concerning WL were obtained from the Estonian Weather Service (Estonian Environment Agency, n.d.). Calculations were made and figures were created using the program Statistica 12.

RESULTS AND DISCUSSION

External nutrient loading

Data about riverine nutrient loading in L. Peipsi *s.l.* were available for 2001–2005 and 2007–2011 (Table 1). The catchment area of the Velikaya River is 2.6 times as large as that of the Emajõgi River and its mean discharge is 2.5 times as high (188 and 75 m³ s⁻¹, respectively). The annual (2001–2011) mean total nitrogen (TN) loading from the Emajõgi River made up 66% of the summary loading from the Estonian side and 35% of the loading in L. Peipsi *s.l.* At the same time, the mean annual TP loading made up 60% of the total loading from the Estonian side and 21% of the loading in L. Peipsi *s.l.* In the same period, the annual mean TN discharge from the Velikaya River constituted 85% of the total loading from the Russian side and 40% of the loading in L. Peipsi *s.l.* While the mean TP loading accounted for 84% of the loading from the Russian side and 54% of the loading in L. Peipsi *s.l.*, then the Velikaya River carried more than half of TP (54%) into L. Pihkva, affecting significantly the water quality in this shallow water body. Also Piirimäe et al. (2015) found that 77 tonnes (34%) of the TP load into L. Pihkva originated in the Estonian part of the catchment and the remaining 148 tonnes (66%) came from Russia.

Comparison of the two periods showed that from the first (2001–2005) to the second (2007–2011) period there was a decrease in the TP loading, which was more obvious in the Emajõgi River (24%) than in the Velikaya River (13%). The total TP loading in L. Peipsi *s.l.* decreased by 19% while the decrease of TN was rather modest, 8% (Table 1). However, from the Russian side the TN load decreased significantly (20%) while from the Estonian side the amount of TN in the riverine load was still high and even showed a slight increase (4%) in the second sub-period (Table 1). Piirimäe et al. (2015) found that in 2006–2010, on the Estonian side, more than 90% of the P load came from diffuse sources while the P load from the Russian side came mainly from point sources. The predominance of diffuse sources can explain the modest decrease in the riverine TN load from the Estonian side.

Table 1. Discharge and riverine loading (TN – total nitrogen, TP – total phosphorus) from two largest rivers to L. Peipsi *s.l.* during 2001–2005 and 2007–2011 (data from Department of Environmental Engineering, Tallinn University of Technology)

	Catchment area, km ²	Period	Discharge, m ³ /s	TN t y ⁻¹	TP t y ⁻¹
Emajõgi R.	9 745	2001–2005	76	5 499	165
		2007–2011	74	5 742	126
<i>Change</i>			–3%	+4%	–24%
Total Estonia	16 323	2001–2005	135	8 324	270
		2007–2011	123	8 680	219
<i>Change</i>			–9%	+4%	–19%
Velikaya R.	25 200	2001–2005	183	6 961	396
		2007–2011	192	6 047	344
<i>Change</i>			+5%	–13%	–13%
Total Russia	28 675	2001–2005	221	8 532	489
		2007–2011	225	6 851	397
<i>Change</i>			+2%	–20%	–19%
L. Peipsi <i>s.l.</i>	44 998	2001–2005	355	16 857	759
		2007–2011	348	15 531	615
<i>Change</i>			–2%	–8%	–19%

Nutrients in lake water

The elements characterizing water quality (TP, TN) were significantly different ($p < 0.001$) for L. Peipsi *s.s.* and L. Pihkva in the two sub-periods. Lake Peipsi *s.s.* was markedly poorer in nutrients and had clearer water than the southern part, L. Pihkva. The most variable quality element, TP, varied significantly for L. Peipsi *s.s.* ($p < 0.001$) and L. Pihkva ($p < 0.01$) in the two sub-

periods. In L. Peipsi *s.s.*, the concentration of TP in the first sub-period varied from 34 to 61 $\mu\text{g L}^{-1}$ and in the second sub-period, from 40 to 50 $\mu\text{g L}^{-1}$ (Table 2). In L. Pihkva, the corresponding values varied from 150 to 180 $\mu\text{g L}^{-1}$ in the first sub-period and from 107 to 148 $\mu\text{g L}^{-1}$ in the second sub-period. Also Carlson's trophic index TSI_{TP} (Carlson, 1977) testified a slight decrease in the trophic state of both lake parts over 2003–2012 (Table 2).

Table 2. Parameters of the trophic status of L. Peipsi *s.s.* and L. Pihkva in the past (1985–1996 geometrical mean of growing season; Starast et al., 2001) and during our study (2003–2007 and 2008–2012)

Parameter	Period	L. Peipsi <i>s.s.</i>	SE	L. Pihkva	SE
Total P, $\mu\text{g L}^{-1}$	1985–1996	35	± 3.86	63	± 3.71
	2003–2007	50	± 1.88	165	± 11.05
	2008–2012	46	± 1.55	124	± 5.94
Total N, $\mu\text{g L}^{-1}$	1985–1996	678	± 27.26	1010	± 44.92
	2003–2007	658	± 20.67	1193	± 36.43
	2008–2012	694	± 29.42	1178	± 44.06
Chlorophyll <i>a</i> , $\mu\text{g L}^{-1}$	1983–1997	14	± 1.03	26	± 3.41
	2003–2007	21	± 1.19	60	± 5.08
	2008–2012	24	± 1.04	74	± 5.67
Secchi depth, m	1983–2000	1.80	± 0.05	1.25	± 0.03
	2003–2007	1.45	± 0.06	0.56	± 0.02
	2008–2012	1.54	± 0.05	0.66	± 0.03
Carlson's TSI _{TP}	2003–2007	59.4	± 0.55	75.4	± 1.21
	2008–2012	58.8	± 0.42	73.4	± 0.53
Carlson's TSI _{Chl_a}	2003–2007	59.3	± 0.61	70.5	± 0.90
	2008–2012	61.2	± 0.45	72.4	± 0.70

The data for August as the month with the poorest ecological state (Lindpere et al., 1990) showed a decrease in the water TP content in both lake parts (Table 2). This demonstrates the ability of the shallow lake's ecosystem to react sensitively to changes in pollution loads (Tammeorg et al., 2013). The mean concentration of TP in L. Pihkva was about three times as high as in L. Peipsi *s.s.*, which allows us to suggest that the influence of L. Pihkva on L. Peipsi *s.s.*, exerted via the connecting L. Lämmijärv (Fig. 1), may be essential (Haberman et al., 2010). Also Buhvestova et al. (2011) found that the major part of the nutrient loading from the south reaches L. Peipsi *s.s.* through L. Lämmijärv. This affected the water quality in L. Peipsi *s.s.* during our study period (2003–2012): the concentration of TP decreased in both lake parts and attained a stable level in the second sub-period (2008–2012), especially in L. Peipsi *s.s.* (Fig. 2).

On the basis of the TP concentration in August, the quality class (these quality classes are worked out for L. Peipsi based on WFD criteria) for L. Peipsi *s.s.* improved from 'Bad' to 'Moderate' and for L. Pihkva, from 'Very bad' to 'Bad' (Table 3), which was accompanied by a lower TP concentration and some dilution effect due to the higher water level in the second sub-period. Despite a certain decline in the TP concentration in the water of both lake parts, it remained still high in L. Pihkva. It is widely recognized that the internal TP loading delays the recovery of shallow lakes from eutrophication (Jeppesen et al., 2005; Søndergaard et al., 2013; Tammeorg et al., 2014). Differences in the nutrient concentrations in the lake parts are also caused by differences in their morphology and catchment area, as well as by different efficiency of wastewater treatment in the catchments. At the end of the 20th century (1985–1996), the mean values of TP content (Starast et al., 2001) were 1.4 times lower ('Moderate') in L. Peipsi *s.s.* and 2.3 times lower ('Bad') in L. Pihkva than in the present study period (Table 2, compare to classification in Table 3). According to Vollenweider and Kerekes (1982), a lake is hypertrophic at a TP water concentration of

$\geq 80 \mu\text{g L}^{-1}$. Thus, L. Peipsi *s.s.* has retained its eutrophic state whereas L. Pihkva has exceeded the threshold for hypertrophy.

Differently from TP, the TN concentration in the water of both lake parts remained relatively stable throughout both sub-periods. The mean values of TN for 1985–1996 (Starast et al., 2001) did not differ significantly from the present data either (Table 2). According to Buhvestova et al. (2011), this may indicate the resilience of the lake to year-to-year changes in the riverine loads of nitrogen. According to the mean TN concentration in August for the two sub-periods (considering also the corresponding data for 1985–1996), the quality class for L. Peipsi *s.s.* and L. Pihkva remained 'Moderate' (Table 3).

Water transparency and water level

During our study period (2003–2012), the SD values slightly increased in both lake parts but were significantly different ($p < 0.001$) for L. Peipsi *s.s.* and L. Pihkva. However, comparable data from the past (1983–2000; Starast et al., 2001) showed a much higher SD for both lake parts (Table 2). With the decreasing SD towards the present, the difference between the northern and southern lake parts increased. Although water transparency decreased in both lake parts, the decrease was significant in L. Pihkva (50%). Considering water clarity, the condition of L. Peipsi *s.s.* remained 'Moderate' and the condition of L. Pihkva remained 'Very bad' throughout the present study (Table 3). However, according to data from 1983–2000 (Starast et al., 2001), the condition of L. Pihkva was 'Moderate' (Table 3).

In L. Peipsi *s.l.*, fluctuations of the natural WL showed an overall range of 3.04 m over the last 80 years, with an average annual range of 1.15 m (Jaani, 2001). Fluctuations in WL may reinforce or diminish the effect of eutrophication (Paerl and Huisman, 2008). In L. Peipsi *s.l.* the WL was somewhat higher in the second sub-period (Fig. 3). This might be one of the drivers for a

Table 3. Boundaries of ecological state classes for lakes Peipsi *s.s.* (PE) and Pihkva (PI) according to physical-chemical quality (total phosphorus – TP; total nitrogen – TN; Secchi depth – SD) value, ranges of geometrical means for ice-free period (Ministry of the Environment, 2009a, 2009b)

Quality indicator	Unit	Very good	Good	Moderate	Bad	Very bad
TP	$\mu\text{g L}^{-1}$	<17 PE	17–25 PE	>25–49 PE	>49–79 PE	>79 PE
		<30 PI	30–50 PI	>50–85 PI	>85–135 PI	>135 PI
TN	$\mu\text{g L}^{-1}$	≤ 300 PE	>300–510 PE	>510–890 PE	>890–1300 PE	>1300 PE
		≤ 490 PI	>490–720 PI	>720–1200 PI	>1200–1600 PI	>1600 PI
SD	m	≥ 3.5 PE	<3.5–2.5 PE	<2.5–1.5 PE	<1.5–1.0 PE	<1.0 PE
		≥ 2.0 PI	<2.0–1.5 PI	<1.5–1.0 PI	<1.0–0.7 PI	<0.7 PI

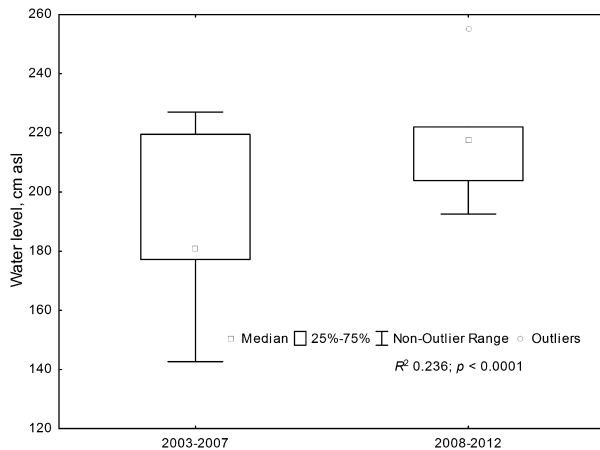


Fig. 3. Water level of *L. Peipsi s.l.* in the two study sub-periods (mean for July–August), asl – above sea level.

slight improvement of the water quality in the lake. Tammeorg et al. (2013) found that the internal load of P in *L. Peipsi s.s.* is several times as high as the external loading, and that this is largely due to the WL and wind speed. The effect of WL, as well as the mechanical influence of the wind and waves, is stronger in the shallower part, *L. Pihkva*, because of its 8 times smaller volume compared with *L. Peipsi s.s.* Kangur et al. (2007) found that periods of accelerated eutrophication in *L. Pihkva* had occurred in dry years with a low WL when the residence time of water in the lake was longer. Their results indicate a strong effect of water temperature and WL on sediment variables (P, N, C, S) with a time lag of 0–5 years.

Response of phytoplankton

Carvalho et al. (2013) recommended *Chla*, phytoplankton trophic index (PTI), and cyanobacterial biomass as three of the strongest metrics for use as robust measures for assessing the ecological quality of lakes in relation to nutrient-enrichment pressures. From among these, we opted for *Chla* and cyanobacterial biomass and, in addition, some other phytoplankton parameters (percentage and dominants of cyanobacteria and chlorophytes and biomass of diatoms) to analyse the state of different parts of *L. Peipsi s.l.* Phytoplankton biomass showed a significant decrease in both lake parts during the second sub-period (2008–2012, Fig. 4), which was caused by a decline of the dominant algal groups, cyanobacteria and diatoms. At the same time, the percentage of cyanobacteria showed a trend of increase in the eutrophic *L. Peipsi s.s.* ($p = 0.005$) and a trend of decrease in the hypertrophic southern parts of the lake ($p = 0.023$). Four cyanobacterial genera (*Gloeotrichia*,

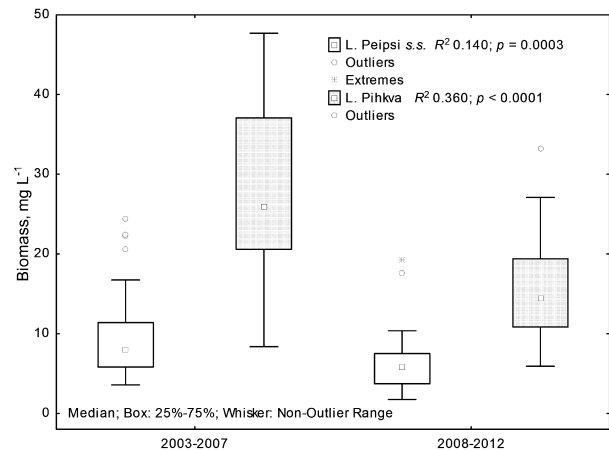


Fig. 4. Biomass of phytoplankton in *L. Peipsi s.s.* and *L. Pihkva* in the two study sub-periods, data for August. Significance of the difference between periods in each lake is shown.

Anabaena, *Aphanizomenon*, and *Microcystis*) were found among the dominants; *Gloeotrichia* and *Anabaena* preferred *L. Peipsi s.s.*, and *Aphanizomenon* and *Microcystis*, *L. Pihkva*. The data for *L. Peipsi* from 1997–2011 (Laugaste et al., 2013) suggest that the principal factor affecting all cyanobacterial genera taken together is temperature (accounting for 33% of the variance), followed by nutrients (27%) and WL (15%). It is widely accepted that higher temperatures promote eutrophication (Battarbee et al., 2012). In *L. Peipsi*, water temperature has increased by 0.32–0.42 degrees per decade (Nõges et al., 2010). During our study period, a drop in *Gloeotrichia echinulata* in *L. Peipsi s.s.* ($p = 0.002$) and a drop in the genus *Microcystis* in *L. Pihkva* ($p = 0.006$) were observed, especially during the second sub-period. The biomass of diatoms showed a decreasing trend in the second sub-period, which was more pronounced for *L. Peipsi s.s.*

The biomass of phytoplankton, cyanobacteria, diatoms, and chlorophytes had negative correlations with summer WL (Fig. 5) in the two sub-periods; correlations for cyanobacteria were stronger for the shallower part ($R^2 = 0.058$ for *L. Peipsi s.s.*, $R^2 = 0.189$ for *L. Pihkva*). Also Nõges et al. (2003) noted that WL is the leading factor controlling the light climate as well as nutrient cycles in shallow lakes. At lower WLs with better light availability, nutrient limitation takes over the control of phytoplankton.

Comparison with earlier data (1983–1997; Starast et al., 2001, Table 2) shows that *Chla* content increased in both lake parts but without a significant difference between the two sub-periods (2003–2007, 2008–2012). According to the mean *Chla* content for August, the quality class of *L. Peipsi s.s.* and *L. Pihkva* remained ‘Bad’ in both periods. According to May et al. (2014),

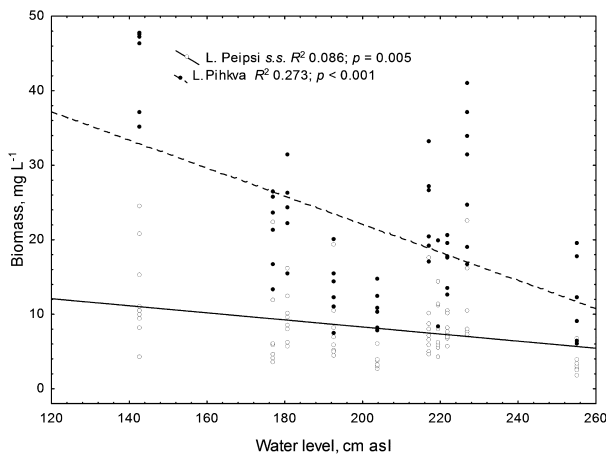


Fig. 5. Correlation between phytoplankton biomass and water level (mean for July–August) in L. Peipsi *s.s.* and L. Pihkva in 2003–2012, asl – above sea level.

the commonly used *Chla* metrics may actually even increase during the early stages of recovery; in the longer term, the expected decline is attained. We noted that although the values of *Chla* did not show significant differences between the two sub-periods, the *Chla*/biomass ratio increased in the second sub-period. Obviously, this is associated with the increasing share of chlorophytes in 2008–2012 ($p = 0.003$ in L. Peipsi *s.s.*, $p = 0.004$ in L. Pihkva). At the same time, the biomass of chlorophytes as well as a group of small algae (consisting of chlorophytes, chrysophytes, cryptophytes, and discoid diatoms) remained at a similar level in both periods. According to Jeppesen et al. (2005), during the recovery process in shallow lakes, shifts in the structure of the phytoplankton community are reflected in the increasing share of diatoms, cryptophytes, and chrysophytes while no significant changes occur in the share of cyanobacteria. In some large lakes of Finland, at a decreased TP concentration and an increased TN : TP ratio, the share of chlorophytes in phytoplankton biomass increased during the last >20 years, and an increase of *Chla* was observed in the majority of the studied 19 lakes (Arvola et al., 2011). In L. Peipsi, the TN : TP ratio as well as the biomass of chlorophytes remained at the same level in the two sub-periods while the increased share of chlorophytes was associated with the decreased biomass of the dominant groups – cyanobacteria and diatoms.

Moderate positive correlations were revealed between phytoplankton variables and nutrient concentrations (stronger and more significant with TP than with TN). Beaulieu et al. (2013) found, using a data set of more than 1000 lakes in the United States, that TN and water temperature provide the best model, which explains 25% of the variance in cyanobacterial biomass. In

L. Peipsi *s.l.*, compared with TN, TP was more strongly associated with phytoplankton and cyanobacterial biomass in the summer data set for 1997–2008 (Haberman et al., 2010). Possibly, the presence of N_2 -fixing cyanobacteria among the dominants camouflaged the relationships of algae with nitrogen in the water, and the amount of nitrogen was sufficient for phytoplankton growth in the lake.

In L. Peipsi *s.s.*, a decreasing trend was found for dissolved inorganic nitrogen, biomass of cyanobacteria, diatoms, and whole phytoplankton, and an increasing trend for *Chla* and the share of chlorophytes and cyanobacteria (mainly owing to the contribution of the genus *Microcystis*). In L. Pihkva, the biomass of cyanobacteria (mainly *Microcystis*), diatoms, and the whole phytoplankton, as well as the share of cyanobacteria, decreased while *Chla* and the share of chlorophytes and the zooplankton/phytoplankton biomass ratio (Fig. 6) increased.

Sas (1989) analysed 18 European lakes and argued that phytoplankton has a four-stage response to reduction in the nutrient loading: the first, no response is found as phosphate concentration is too high throughout the growing season to limit phytoplankton growth; the second, P-limitation occurs during part of the summer, leading to lower phytoplankton biomass per unit volume but no changes in biomass per unit area; the third, biomass per unit area is affected; and the fourth, changes occur also in the composition of the phytoplankton community. In terms of the above theory, the phytoplankton of L. Peipsi *s.l.* showed some signs of recovery during the ten-year period (at the second or third stage): the biomass of phytoplankton and cyanobacteria decreased significantly in both lake parts with a clearer trend of

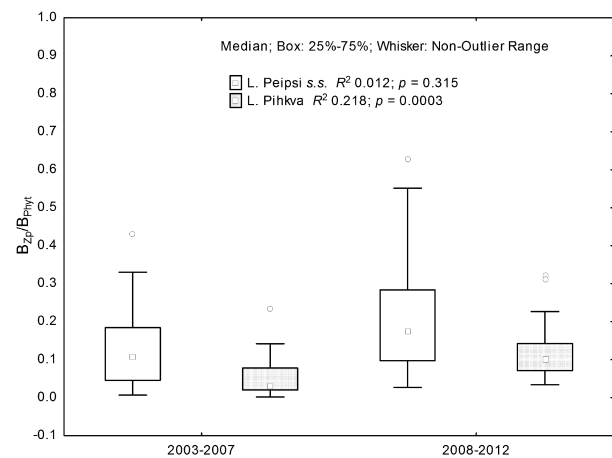


Fig. 6. The zooplankton to phytoplankton biomass ratio (B_{Zp}/B_{Phyt}) for L. Peipsi *s.s.* and for L. Pihkva in the two study sub-periods, data for August. Significance of the difference between periods in each lake is shown.

improvement in the hypertrophic L. Pihkva than in the eutrophic L. Peipsi *s.s.* The comparison of two sub-periods revealed that in L. Pihkva, the biomass value of phytoplankton was twice lower and the biomass value of cyanobacteria was 2.4 times lower in the second study sub-period. In this shallower lake, the lower nutrient load and higher WL (a clearly differing environmental parameter for the two periods) had a much stronger effect on water nutrients and biota compared with the deeper L. Peipsi *s.s.* Despite the decrease in the TP concentration in the water, cyanobacteria were still among the dominants in both lake parts.

Response of zooplankton

It is well known that zooplankton responds to changes in the trophic state of a water body with a certain lag, which may last even several decades (Jeppesen et al., 2002, 2005; Gunn et al., 2012). In the present study, zooplankton data did not show a clear response to changes in the pollution load or in-lake nutrient concentrations in L. Peipsi *s.l.* Rather, these data indicate the continuation of the eutrophication process in both lake parts (Table 4). Jeppesen et al. (2002) argued that the response of zooplankton to reduced TP is stronger at the species level. Analysis of the indicative parameters of zooplankton in L. Peipsi *s.l.* showed that in both lake parts, there was an increase in the abundance of species indicating eutrophy (Piasecki and Wolska, 2007; Haberman and Haldna, 2014): *Keratella tecta* (7-fold increase in L. Peipsi *s.s.* as well as in L. Pihkva), *Trichocerca rousseleti* (7-fold and 35-fold increase, respectively), and *Chydorus sphaericus* (3-fold and 2-fold

increase, respectively; Table 4). In L. Peipsi *s.s.* a decrease was observed in the abundance of the rotifer *Conochilus unicornis* (Table 4), favouring lower trophic state (Gunn et al., 2012; Haberman and Haldna, 2014). At the same time, it was absent from L. Pihkva. Several zooplankton species (*Kellicottia longispina*, *Bosmina berolinensis*, and *Bythotrephes longimanus*) characteristic of oligomesotrophic waters (Haberman and Haldna, 2014) became rare in L. Peipsi *s.l.* The mean zooplankton weight and mean cladoceran weight decreased in L. Peipsi *s.s.* as well as in L. Pihkva (Table 4). The mean zooplankton weight decreases with increasing trophicity (Jeppesen et al., 2010).

However, there are other slight signs suggesting some recovery of the lake. First, in L. Peipsi *s.s.*, the abundance of rotifers and their share in the total zooplankton abundance decreased (Table 4). Rotifers have a high potential as bioindicators of a lake's trophic state and water quality (Ejsmont-Karabin, 2012; Haberman and Haldna, 2014). May et al. (2014) even emphasized that rotifers may respond more rapidly to changes in a lake's trophic state than TP and Chl_a concentrations. Second, the abundance of the genus *Daphnia* and its mean individual weight increased a little in L. Peipsi *s.s.* (Table 4). The grazing rate of herbivorous zooplankton is an indicator of the trophic state of the lake, which increases in parallel with decreasing trophic level (Agasild et al., 2007). The increase of the genus *Daphnia*, noted also by Jeppesen et al. (2002), may be among the causes of the reduction in phytoplankton biomass (Fig. 4), as well as of the increase of the zooplankton/phytoplankton biomass ratio (Fig. 6). An increase in the mean cladoceran size and an elevated share of *Daphnia*

Table 4. Mean zooplankton parameters changes in eutrophic L. Peipsi *s.s.* and hypertrophic L. Pihkva in August during two periods, significance of differences between periods. Abbreviations: Ab – abundance, Mw – mean weight, thous. ind – thousand individuals, ns – not significant

Parameter	Peipsi			Pihkva		
	2003–2007	2008–2012	<i>P</i> value	2003–2007	2008–2012	<i>P</i> value
Ab of rotifers, thous. ind. m ⁻³	94	65	ns	49	146	0.007
Share (%) of rotifers in zooplankton Ab	41	31	ns	27	37	ns
Ab of <i>Keratella tecta</i> , thous. ind. m ⁻³	1	7	ns	8	59	0.007
Ab of <i>Trichocerca rousseleti</i> , thous. ind. m ⁻³	0.1	0.5	ns	0.2	7	ns
Ab of <i>T. similis</i> , thous. ind. m ⁻³	0.2	5	ns	6	26	ns
Ab of <i>Conochilus unicornis</i> , thous. ind. m ⁻³	6	0.6	ns	0	0	
Ab of <i>Chydorus sphaericus</i> , thous. ind. m ⁻³	4	11	0.007	49	74	ns
Share (%) of <i>C. sphaericus</i> in cladoceran Ab	20	30	ns	30	77	0.005
Share (%) of <i>C. sphaericus</i> in zooplankton Ab	3	6	0.018	18	21	ns
Mw of <i>Daphnia</i> individual, µg	39.1	44.5	ns	32.9	22.1	ns
Ab of genus <i>Daphnia</i> spp. thous. ind. m ⁻³	3.5	4.8	ns	15.9	10.4	ns
Share (%) of <i>Daphnia</i> spp. in cladoceran Ab	37	32	ns	55	10	<0.0001
Mw of zooplankton individual, µg	8.9	6.3	0.034	6.4	4.5	ns
Mw of cladoceran individual, µg	38.1	32.6	ns	17.4	8.4	0.013

in the total cladoceran abundance or biomass are often reflections of a reduced predation on zooplankton (Jeppesen et al., 2005; Carvalho et al., 2012). This may also be the case in Lake Peipsi. In L. Peipsi *s.l.*, the stocks of planktivorous vendace and smelt decreased since the early 1990s and had not yet recovered by the 2000s (Kangur et al., 2008). Third, the share of calanoids (mainly *Eudiaptomus gracilis*) in the total copepod abundance increased in both lake parts (Table 4). Although *E. gracilis* is generally known to be a species of lower trophic (Gunn et al., 2012; Haberman and Haldna, 2014), Riccardi and Rossetti (2007) found that *E. gracilis* is tolerant of a wide range of trophic conditions in many eutrophic water bodies in Italy. In L. Peipsi, *E. gracilis* has always been a favoured food object for planktivorous fishes (Ibneeva, 1983), and its modest increase may be caused by a decrease in fish pressure. Fourth, the zooplankton to phytoplankton biomass ratio (B_{Zp}/B_{Phyt}) increased in both lakes while the increase was significant in the shallower L. Pihkva (Fig. 6). The B_{Zp}/B_{Phyt} ratio decreases in parallel with increasing TP content in lakes (Blank et al., 2010; Jeppesen et al., 2010). Hence this parameter can be used for the evaluation of the trophic of a water body and its ecosystem.

CONCLUSION

Comparison of the two study sub-periods (2003–2007 and 2008–2012) demonstrated a decline of nutrients in loadings to L. Peipsi *s.l.*, and also in in-lake water, showing a small shift towards the recovery of the lake. The biomass of phytoplankton and cyanobacteria decreased while cyanobacteria remained still dominant in phytoplankton. Compared to phytoplankton, changes in zooplankton were not so clear. The amount of indicator species and mean zooplankton weight reflected a continuous eutrophication process while changes in the amount of rotifers and the genus *Daphnia* indicated a subtle shift towards recovery. We conclude that the main reasons for the limited recovery of L. Peipsi are the following: (1) reduction of pollution load into L. Peipsi *s.l.* was modest to attain significant changes in its ecosystem; (2) continuously too high nutrient concentration (effect of internal loading) in the water of the studied lake parts; (3) reinforcing impact of climate warming on the ongoing eutrophication; (4) ten-year period was too short for attaining a definite recovery of the lake. As biotic communities differed in the timing of their responses to changing nutrient conditions, the recovery may be a slow process.

ACKNOWLEDGEMENTS

This research was supported by the Estonian University of Life Sciences (base funding project P15021). Data collection within the frames of the state monitoring programme was supported by the Estonian Ministry of the Environment. Special thanks are due to Mrs Ester Jaigma for revising the English text of the manuscript. The contribution of the anonymous referees is highly appreciated.

The publication costs of this article were covered by the Estonian Academy of Sciences.

REFERENCES

- Agasild, H., Zingel, P., Tönno, I., Haberman, J., and Nöges, T. 2007. Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). *Hydrobiologia*, **584**, 167–177.
- Arvola, L., Järvinen, M., and Tulonen, T. 2011. Long-term trends and regional differences of phytoplankton in large Finnish lakes. *Hydrobiologia*, **660**, 125–134.
- Battarbee, R. W., Anderson, N. J., Bennion, H., and Simpson, G. L. 2012. Combining limnological and palaeolimnological data to disentangle the effects of nutrient pollution and climate change on lake ecosystems: problems and potential. *Freshwater Biol.*, **57**, 2091–2106.
- Beaulieu, M., Pick, F., and Gregory-Eaves, I. 2013. Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. *Limnol. Oceanogr.*, **58**, 1736–1746.
- Bennion, H., Simpson, G. L., and Goldsmith, B. J. 2015. Assessing degradation and recovery pathways in lakes impacted by eutrophication using the sediment record. *Front. Ecol. Evol.*, **3**, 1–20.
- Blank, K., Laugaste, R., and Haberman, J. 2010. Temporal and spatial variation in the zooplankton : phytoplankton biomass ratio in a large shallow lake. *Estonian J. Ecol.*, **59**, 99–115.
- Buhvestova, O., Kangur, K., Haldna, M., and Möls, T. 2011. Nitrogen and phosphorus in Estonian rivers discharging into Lake Peipsi: estimation of loads and seasonal and spatial distribution of concentrations. *Estonian J. Ecol.*, **60**, 18–38.
- Carlson, R. E. 1977. A trophic State Index for lakes. *Limnol. Oceanogr.*, **22**, 361–369.
- Carvalho, L., Miller, C., Spears, B. M., Gunn, I. D. M., Bennion, H., Kirika, A., and May, L. 2012. Water quality of Loch Leven: responses to enrichment, restoration and climate change. *Hydrobiologia*, **681**, 35–47.
- Carvalho, L., Poikane, S., Lyche Solheim, A., Phillips, G., Borics, G., Catalan, J., et al. 2013. Strength and uncertainty of phytoplankton metrics for assessing eutrophication impacts in lakes. *Hydrobiologia*, **704**, 127–140.
- Dokulil, M. T. and Teubner, K. 2005. Do phytoplankton communities correctly track trophic changes? An

- assessment using directly measured and palaeolimnological data. *Freshwater Biol.*, **50**, 1594–1604.
- Ejsmont-Karabin, J. 2012. The usefulness of zooplankton as lake ecosystem indicators: rotifer trophic index. *Pol. J. Ecol.*, **60**, 339–350.
- EU. 2000. EU Directive 2000/60/EC establishing a framework for community action in the field of water policy. *Official Journal of the European Communities*, **L327**, 1–73.
- European Commission. 2009. *Common Implementation Strategy for the Water Framework Directive (2000/60/EC), Guidance Document No. 20, Guidance Document on Exemptions to the Environmental Objectives. Technical report 2009-027*. Office for Official Publications of the European Communities, Luxembourg.
- Glenk, K., Lago, M., and Moran, D. 2011. Public preferences for water quality improvements: implications for the implementation of the EC Water Framework Directive in Scotland. *Water Policy*, **13**, 645–662.
- Gunn, I. D. M., O'Hare, M. T., and Maitland, P. S. 2012. Long-term trends in Loch Leven invertebrate communities. *Hydrobiologia*, **681**, 59–72.
- Haberman, J. 2001. Zooplankton. In *Lake Peipsi. Flora and Fauna* (Pihu, E. and Haberman, J., eds), pp. 50–68. Sulemees Publishers, Tartu.
- Haberman, J. and Haldna, M. 2014. Indices of zooplankton community as valuable tools in assessing the trophic state and water quality of eutrophic lakes: long term study of lake Võrtsjärv. *J. Limnol.*, **73**, 1–23.
- Haberman, J., Haldna, M., Laugaste, R., and Blank, K. 2010. Recent changes in large and shallow Lake Peipsi (Estonia/Russia): causes and consequences. *Pol. J. Ecol.*, **58**, 645–662.
- Ibneeva, N. I. 1983. Exploitation of food resources by planktophagous fishes in Lake Peipsi-Pihkva. *Sbornik nauchnykh trudov GosNIORKh*, **209**, 44–50 (in Russian).
- Jaani, A. 2001. Hydrological regime and water balance. In *Lake Peipsi: Meteorology, Hydrology, Hydrochemistry* (Nõges, T., ed.), pp. 38–72. Sulemees Publishers, Tartu.
- Jeppesen, E., Jensen, J.-P., and Søndergaard, M. 2002. Response of phytoplankton, zooplankton, and fish to re-oligotrophication: an 11 year study of 23 Danish lakes. *Aquat. Ecosyst. Health Manage.*, **5**, 31–43.
- Jeppesen, E., Søndergaard, M., Jensen, J.-P., Havens, K. E., Anneville, O., Carvalho, L., et al. 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshwater Biol.*, **50**, 1747–1771.
- Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S. A. J., et al. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia*, **646**, 73–90.
- Johnson, R. K. and Angeler, D. G. 2010. Tracing recovery under changing climate: response of phytoplankton and invertebrate assemblages to decreased acidification. *J. N. Am. Benthol. Soc.*, **29**, 1472–1490.
- Kangur, M., Kangur, K., Laugaste, R., Punning, J.-M., and Möls, T. 2007. Combining limnological and palaeolimnological approaches in assessing degradation of Lake Pskov. *Hydrobiologia*, **584**, 121–132.
- Kangur, A., Kangur, P., Pihu, E., Vaino, V., Tambets, M., Krause, T., and Kangur, K. 2008. Kalad ja kalapüük. In *Peipsi* (Haberman, J., Timm, T., and Raukas, A., eds), pp. 317–340. Eesti Loodusfoto, Tartu (in Estonian).
- Kangur, K., Kangur, P., Ginter, K., Orru, K., Haldna, M., Möls, T., and Kangur, A. 2013. Long-term effects of extreme weather events and eutrophication on the fish community of shallow Lake Peipsi (Estonia/Russia). *J. Limnol.*, **72**, 376–387.
- Laugaste, R., Nõges, T., Nõges, P., Jastremskij, V. V., Milius, A., and Ott, I. 2001. Algae. In *Lake Peipsi: Flora and Fauna* (Pihu, E. and Haberman, J., eds), pp. 31–49. Sulemees Publishers, Tartu.
- Laugaste, R., Panksep, K., and Haldna, M. 2013. Dominant cyanobacterial genera in Lake Peipsi (Estonia/Russia): effect of weather and nutrients in summer months. *Estonian J. Ecol.*, **62**, 229–243.
- Lindpere, A., Starast, H., Milius, A., and Saan, T. 1990. Peipsi-Pihkva järve vee omaduste muutumine maist septembrini. In *Peipsi järve seisund* (Timm, T., ed.), pp. 10–11. Eesti Teaduste Akadeemia, Zooloogia ja Botaanika Instituut, Tartu (in Estonian).
- Loigu, E. and Leisk, Ü. 1996. Water quality of rivers in the drainage basin of Lake Peipsi. *Hydrobiologia*, **338**, 25–35.
- Loigu, E., Leisk, Ü., Iital, A., and Pachel, K. 2008. Peipsi järve valgla reostuskoormus ja jõgede kvaliteet. In *Peipsi* (Haberman, J., Timm, T., and Raukas, A., eds), pp. 179–199. Eesti Loodusfoto, Tartu (in Estonian).
- Mao, F. and Richards, K. 2012. Irreversible river water quality and the concept of the reference condition. *Area*, **44**, 423–431.
- May, L., Spears, B. M., Dudley, B. J., and Gunn, I. D. M. 2014. The response of the rotifer community in Loch Leven, UK, to changes associated with a 60% reduction in phosphorus inputs from the catchment. *Int. Rev. Hydrobiol.*, **99**, 65–71.
- Ministry of the Environment. 2009a. Procedure for the Establishment of Bodies of Surface Water and a List of the Bodies of Surface Water the State of Which is to be Established, Classes of the States and the Values of Quality Indicators Corresponding to These State Classes, and the Procedure for the Establishment of the Classes of State. *Riigi Teataja*, 2009, 64, 941.
- Ministry of the Environment. 2009b. Order from 28.07.2009, No. 44. www.riigiteataja.ee/akt/13210253 (accessed 2016-11-11).
- Nõges, T., Nõges, P., and Laugaste, R. 2003. Water level as the mediator between climate change and phytoplankton composition in a large shallow temperate lake. *Hydrobiologia*, **506–509**, 257–263.
- Nõges, T., Tuvikene, L., and Nõges, P. 2010. Contemporary trends of temperature, nutrient loading and water quality in large lakes Peipsi and Võrtsjärv, Estonia. *Aquat. Ecosyst. Health Manage.*, **13**, 143–153.
- Paerl, H. W. and Huisman, J. 2008. Blooms like it hot. *Science*, **320**, 57–58.
- Piasecki, W. G. and Wolska, M. 2007. Pelagic zooplankton as an indicator of lake Pełcz (Westpomerania, Poland) trophic state. *Limnol. Rev.*, **7**, 213–218.
- Piirimäe, K., Loigu, E., Pachel, K., and Iital, A. 2015. Virtual mapping of reference conditions of pollutant load in

- water bodies: phosphorus in the Lake Peipsi basin. *Boreal Environ. Res.*, **20**(3), 391–402.
- Räike, A., Pietiläinen, O. P., Rekolainen, S., Kauppila, P., Pitkänen, H., Niemi, J., et al. 2003. Trends of phosphorus, nitrogen, and chlorophyll *a* concentrations in Finnish rivers and lakes in 1975–2000. *Sci. Total Environ.*, **310**, 47–59.
- Riccardi, N. and Rossetti, G. 2007. *Eudiaptomus gracilis* in Italy: how, where and why? *J. Limnol.*, **66**, 64–69.
- Sas, H. 1989. *Lake Restoration by Reduction of Nutrient Loading. Expectation, Experiences, Extrapolation.* Acad. Ver. Richardz GmbH., Germany.
- Søndergaard, M., Bjerring, R., and Jeppesen, E. 2013. Persistent internal phosphorus loading during summer in shallow eutrophic lakes. *Hydrobiologia*, **710**, 95–107.
- Starast, H., Milius, A., Möls, T., and Lindpere, A. 2001. Hydrochemistry of Lake Peipsi. In *Lake Peipsi: Meteorology, Hydrology, Hydrochemistry* (Nõges, T., ed.), pp. 97–131. Sulemees Publishers, Tartu.
- Tammeorg, O., Niemistö, J., Möls, T., Laugaste, R., Panksep, K., and Kangur, K. 2013. Wind-induced sediment resuspension as a potential factor sustaining eutrophication in large and shallow Lake Peipsi. *Aquat. Sci.*, **75**, 559–570.
- Tammeorg, O., Möls, T., and Kangur, K. 2014. Weather conditions influencing phosphorus concentration in the growing period in the large shallow Lake Peipsi (Estonia/Russia). *J. Limnol.*, **73**, 11–19.
- Verschuren, D., Johnson, T. C., Kling, H. J., et al. 2002. History and timing of human impact on Lake Victoria, East Africa. *R. Soc.*, **269**, 289–294.
- Vollenweider, R. A. and Kerekes, J. 1982. *Eutrophication of Waters – Monitoring, Assessment and Control. Synthesis Report.* OECD, Paris.
- Yan, N. D., Leung, B., Keller, W., Arnott, S. E., Gunn, J. M., and Raddum, G. G. 2003. Developing conceptual frameworks for the recovery of aquatic biota from acidification. *Ambio*, **32**, 165–169.

Peipsi järve ökoloogiline seisund: kas paranenud, stabiliseerunud või halvenenud?

Kätlin Blank, Enn Loigu, Reet Laugaste ja Juta Haberman

Peipsi (*s.l.*, 3555 km²) järve ökoloogilise seisundi hindamiseks uuriti kahel perioodil (2003–2007 ja 2008–2012) järve kaht vastandlikku osa: lõunapoolset, väiksemat (708 km²) ja enim reostatud Pihkva järve, ning põhjapoolset, suuremat (2611 km²) ja puhtama veega Peipsi Suurjärve. Analüüsi järve ja selle sissevoolude vee kvaliteedi olulisi näitajaid: üldfosfori (TP) ja üldlämmastiku (TN) sisaldust ning vee läbipaistvust. Tähelepanu all oli ka veetase. Perioodide võrdlus näitas, et nii sissevoolude (tabel 1) kui ka järve vee fosforisisaldus (tabel 2) vähenes mõlemas järveosas, viidates järve tervisliku seisundi paranemisele. Sellele võis mõningal määral kaasa aidata ka teise perioodi kõrgem veetase. Muutustele reageeris fütoplanktoni (sh sinivetikate) biomass, mis vähenes teisel uurimisperiodil märkimisväärselt, eriti Pihkva järves (joonis 4). Kuna zooplankton reageerib järve seisundi muutustele viibega (läbi fütoplanktoni), olid muutused zooplanktonis vastuolulised (tabel 4). Zooplanktoni troofsust näitavate indikaatorliikide arvukus ja troofsuse indikaatorina kasutatav zooplankteri keskmine kaal viitasid mõlema järveosa (eriti Pihkva järve) seisundi jätkuvalle eutrofeerumisele. Keriloomade arvukuse vähenemine ja perekond *Daphnia* liikide arvukuse suurenemine Suurjärves peegeldas selle järveosa seisundi tagasihoidlikku paranemist, mida ei leitud Pihkva järves. Kokkuvõttena võib öelda, et kümneaastasel uurimisperiodil ei leitud Peipsi järve seisundi oodatud paranemist. Põhjusteks peame: 1) reostuskoormuse vähenemine ei olnud ökosüsteemi suuremateks muutusteks küllaldane, 2) biogeenide sisaldus järve vees jäi ilmselt suure sisekoormuse ja ka vee soojenemise tõttu jätkuvalt kõrgeks, 3) võimalik, et kümneaastane periood võib olla lühike suuremateks muutusteks planktonis, eriti zooplanktonis.