



Response of primary producers to water level fluctuations of Lake Peipsi

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Abstract. The amplitude of natural fluctuation between annual averages of the water level (WL) of Lake Peipsi (3555 km²) is 1.5 m. A study aimed to examine the impact of WL fluctuations on phytoplankton, macrophytes, and their epiphyton was performed annually at littoral stations during 2005–2015. Also the characteristics of pelagic water were collated with the WL. Changes in littoral and pelagial phytoplankton were similar, with the exclusion of massive wind-caused accumulations of cyanobacteria in the littoral. At the lowest WL a significant increase occurred in (a) the biomass of phytoplankton and the share of phytoplankton-derived organic carbon in water and (b) the species richness and biomass of macrophytes, including submerged plants and macroalgae. The abundance of epiphytes did not reveal a clear relation with the WL. The ratios of biomasses in the years with the lowest and the highest average WL were 2.2 for *Potamogeton* spp. and 2.6 for phytoplankton. The assessment of ecological status at the minimum and the maximum WL differs at least by one quality class. Decisions about ecological status based on phytoplankton and large filamentous green algae at low water may be contrary to decisions based on macrophytes: high biomasses of phytoplankton and macroalgae indicate hypertrophic status, but species-rich macrovegetation and high biomasses of charophytes and elodeids are considered to be characteristic of meso- to eutrophic water bodies.

Key words: limnology, water level, phytoplankton, macrophytes, epiphytes, biomass, ecological assessment.

1. INTRODUCTION

Water bodies are monitored with the aim to evaluate their ecological quality based on the response of aquatic bioindicators to a variety of changes. Among the factors controlling the functioning of water ecosystems, the extent, frequency, and duration of fluctuations in water level (WL) have been considered as very important. There is a large demand for information on lakes with fluctuating WL and their aquatic–terrestrial transition zone (Wantzen et al., 2008). Most of the studies on biological responses to the water level fluctuations (WLF) in lakes concern macrophytes (Leira and Cantonati, 2008). However, data on the impact of natural WLF on macro-

phytes are limited. Furthermore, studies dealing with relationships between epiphytic algae and WLF are scarce (e.g. Rodusky, 2010; Blanco et al., 2014; Zhang et al., 2015), and studies on littoral phytoplankton are extremely rare (Schweizer, 1997; Protopopova, 2003).

On the basis of several studies, it was concluded that WLF cause shifts between the clear and turbid state independently of the nutrient enrichment and top-down effects (Coops et al., 2003; Scheffer and Van Nes, 2007; Bakker and Hilt, 2016). It is probable that in shallow lakes the low WL plays a role that is similar to anthropogenic eutrophication (Moss et al., 2011). Kangur et al. (2007) found in a sediment study that high temperatures and low WL (especially in spring) result in an increased accumulation of organic matter, comparable to eutrophication. A low WL in spring promotes the

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development of submerged vegetation (Beklioglu et al., 2006; Mäemets et al., 2006). According to Coops and Van Geest (2005), lake bottom exposure during a prolonged low water increases submerged vegetation. In contrast, in extremely shallow lakes (average depth ≤ 2 m) submerged macrophytes are supported by higher and more stable WLs (Cobbaert et al., 2015).

The linking of epiphytes to numerous abiotic and biotic factors complicates the understanding of the pattern of their occurrence. Our knowledge of lentic (standing water) epiphyton (EP) communities is less adequate than that of lotic (flowing water) and far less adequate than our knowledge of phytoplankton biology (Lowe, 1996). Many studies carried out on streams have reported a positive impact of a low WL on EP. However, finding relevant data for lakes is problematic. According to Rodusky (2010), a maximum EP biomass and a high nutrient storage in shallow subtropical and tropical lakes can occur only at consistently low WLs. The effect of WL on the amount of EP is closely connected to the growing depth of the host plant, and the effect of growing depth on EP is commonly associated with light (Wetzel, 2001 and references therein; Sánchez et al., 2013; Zhang et al., 2015). The position of EP on the host plant, as well as the common top-down control of EP by a fish–macrozoobenthos cascade may outweigh the impact of WL on EP (Jones and Sayer, 2003).

Generalizing data on a very large scale, Wetzel (1992) concluded: ‘...in lakes and streams, more than 90% of decomposition in the ecosystem is by bacteria utilizing dissolved organic matter (DOM) from non-pelagic sources of primary productivity’. Wetzel also suggested that although it is slow, the decomposition of wetland and littoral DOM is dominating also in the pelagic zone. Therefore, the changes in the littoral production due to WLF may have extensive consequences for the whole lake.

The monitoring of the unregulated large shallow Lake Peipsi included the years with very different WLs: close to the absolute minimum as well as close to the absolute maximum. The observations led to the following hypothesis: a low WL results in a significant increase in the occurrence and biomass of lake primary producers, causing differences in the assessment of the ecological status in comparison with high-water years.

2. MATERIAL AND METHODS

2.1. Site description

The area of Lake Peipsi, located on the border of Estonia and Russia, is 3555 km², with a mean depth of

7.1 m and a maximum depth of 15.3 m. The lake consists of three parts: the largest (87% of the lake volume) and deepest (mean 8.3 m) eutrophic northern part Lake Peipsi *sensu stricto* (Peipsi *s.s.*), the hypertrophic southern part Lake Pihkva (11%; mean depth 3.8 m), and the intermediate, river-like Lake Lämmijärv (2%; mean depth 2.5 m) (Fig. 1). The averaged values of water quality characteristics for the Estonian part of lakes Peipsi *s.s.* and Lämmijärv are presented in Table 1 (extracted from the database of the Estonian State Monitoring Programme).

The shores are predominantly sand, but till, sandstone cliff, peat, and clay also border the lake. The WL is unregulated; the amplitude of fluctuation in its annual averages in 1890–2005 was 1.5 m and the mean WL was 30 m above sea level (a.s.l.) (Jaani, 2001; Jaani et al., 2008). The numbers in the figures below are related to the benchmark value of 28 m a.s.l., i.e. 200 cm above the benchmark = 30 m a.s.l. The average volume of the whole lake is 25.1 km³ and the residence time of water is about two years. The volume of Peipsi at its maximum WL (31 m a.s.l.) is 28.91 km³, and at the minimum WL (29 m a.s.l.) 21.57 km³ (calculations by A. Jaani). For the characterization of annual oscillations we present average water levels of April–May in 1990–2015 (Fig. 2). Spring is the time of the highest WLs (Fig. 3). A permanent ice cover usually forms at the beginning of December and lasts on average 118 days (Jaani et al., 2008). The water is the clearest in June, owing to the low content of phytoplankton at this time. The impact of the waves is substantial due to the long fetches.

Two major wetland districts are neighbouring Lake Peipsi (Fig. 1). The mires of the Peipsi Lowland, which make up about 40% of the Estonian part of the lowland, drain all into the lake (Arold, 2005). Extrapolation of this percentage to the whole lowland gives about 900 km². The Alutaguse Lowland drains only partially into Peipsi. In the whole catchment area of Peipsi, wetlands account for 3.4% (1520 km²) of the total 44 725 km² (Piirimäe et al., 2015).

The data on the WL and temperatures for our study were obtained from the Estonian Weather Service of the Estonian Environment Agency. The WL measurements were made at the Mustvee Hydrometric Station (58°50′51″ N, 26°57′04″ E) on the northwestern shore of Peipsi *s.s.* and at Mehikoorma Hydrometric Station (58°13′57″ N, 27°28′32″ E) on the western shore of Lämmijärv.

Calculations based on satellite images and on the basic map’s depiction of the water edge showed that the area of reeds (mainly *Phragmites australis* (Cav.) Trin. ex Steud.) inside the lake borders made up about 1% of the lake area in 2013 (Peterson and Liira, 2016). This

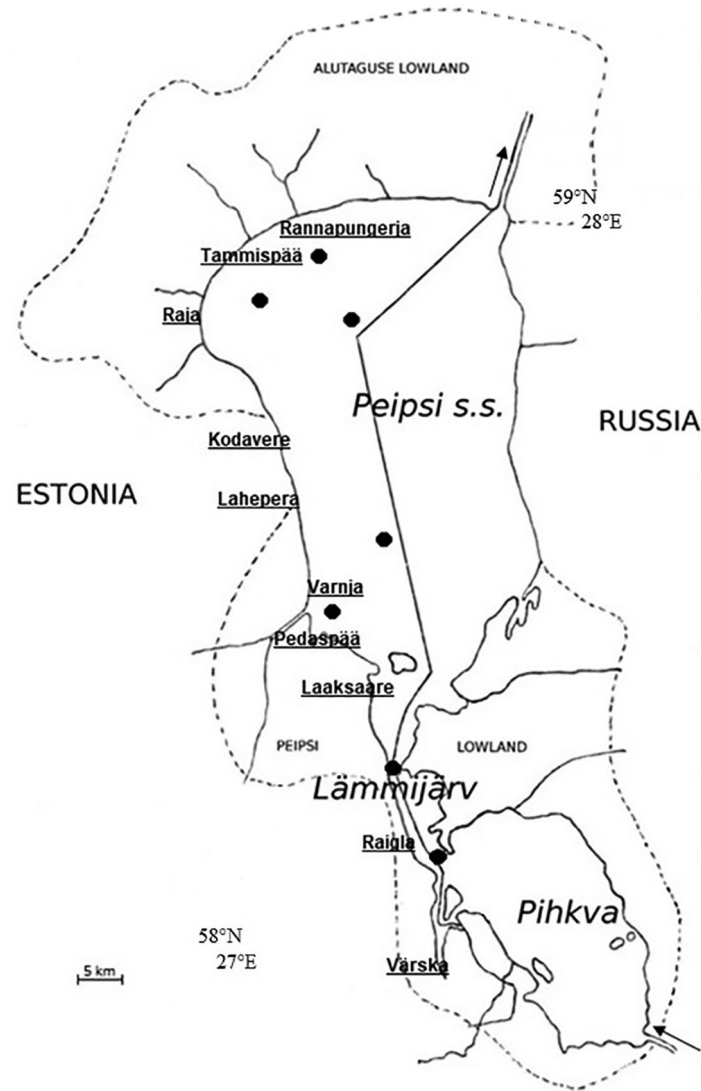


Fig. 1. Lake Peipsi with lowlands (bordered with dashed lines; redrawn from Karukäpp (2008)); pelagic sampling stations in 1997–2015 (black dots), and littoral study stations in 2005–2015 (underlined names).

Table 1. Averaged water quality characteristics (\pm SE) in the Estonian side of the two parts of Lake Peipsi (Peipsi s.s. and Lämmijärv) for the growing period, May to October, in 2005–2015

Water variable	Peipsi s.s. <i>n</i> = 325	Lämmijärv <i>n</i> = 132
Water transparency, SD (m)	1.8 (\pm 0.04)	0.96 (\pm 0.002)
Total phosphorus ($\mu\text{g L}^{-1}$)	36 (\pm 1.6)	70 (\pm 3)
Total nitrogen ($\mu\text{g L}^{-1}$)	710 (\pm 15)	911 (\pm 27)
Phytoplankton chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	18.5 (\pm 0.7)	39 (\pm 2)
Water colour (CNR, °)	42.5 (\pm 1.5)	72.8 (\pm 2.7)
Chemical oxygen demand, CODCr (mg O L^{-1})	29.5 (\pm 0.6)	38.4 (\pm 1.1)

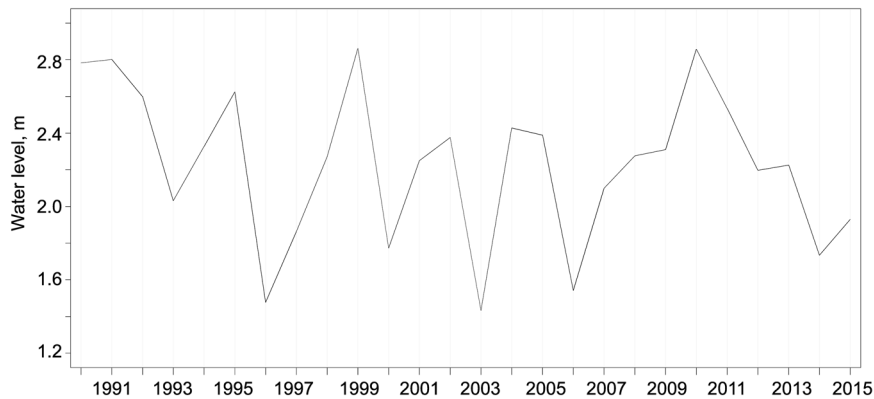


Fig. 2. Long-term dynamics of the average spring water level (April–May) of Lake Peipsi.

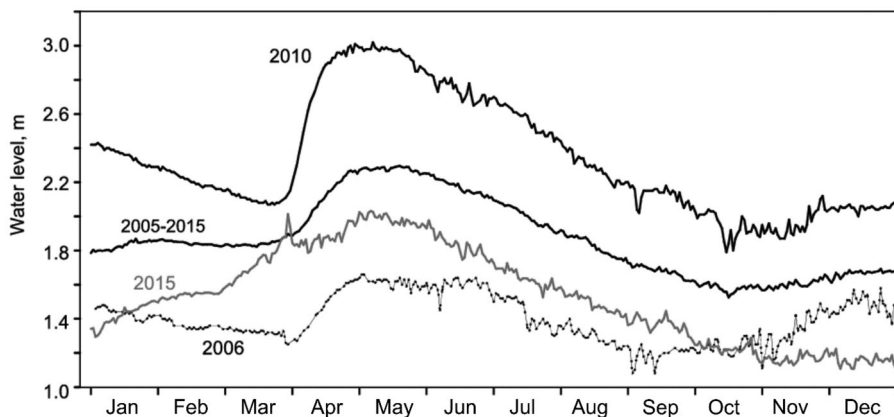


Fig. 3. Seasonal dynamics of the water level of Lake Peipsi in some extreme years and its averaged course in 2005–2015.

is close to the calculation based on the results of field studies from the 2000s (Mäemets and Freiberg, 2004): multiplying the mean width of reeds (90 m) by the length of the lake shore (520 km) yields 47 km² and constitutes 1.3% of the lake area. This belt area serves as the basis for further calculations.

The main submerged plants *Potamogeton perfoliatus* L., *Potamogeton pectinatus* L., *Potamogeton lucens* L., and *Myriophyllum spicatum* L. grow mostly on the lake's side of the reed belt. The maximum growing depth of the dominating *P. perfoliatus* reaches 4 m at some sampling stations, and its scattered stands may occur at a distance of 1–1.5 km from the shore. However, for the calculations of the biomass of pondweeds and macroalgae we used a hypothetical 'compressed' belt width of 20 m between the reed belt and the open lake, assuming that this zone of 10 km² is under water all the time and that in the most favourable years it is covered by submerged stands more or less continuously.

2.2. Pelagic data

The monitoring of the pelagic area was carried out at five stations in Peipsi *s.s.* and at two stations in Lämmijärv (Fig. 1). Water transparency (Secchi depth, SD) was measured and hydrochemical as well as phytoplankton samples were collected monthly during the growing season in 1997–2015. Chemical variables: total phosphorus, orthophosphate, total nitrogen, dissolved inorganic nitrogen, chemical oxygen demand, and water colour were analysed at Tartu Laboratory of the Estonian Environmental Research Centre. Integrated phytoplankton samples were collected through the entire water column. In order to find out the percentage of carbon content in phytoplankton (the main source of autochthonous carbon) in the total organic carbon (TOC) in the pelagic water, we transformed the phytoplankton biomass (FBM) to carbon as approximately 10% of the FBM wet weight (Vollenweider et al., 1974) and TOC on average as 33%

of the chemical oxygen demand (cf. ww/EUR-Lex – 32012DO135 – EN – EUR-Lex.html).

2.3. Littoral data

Fieldwork was carried out annually at ten stations in the littoral zone of the lake (Fig. 1) in the second half of July or in the first half of August 2005–2015. The width of the reed belt was measured with a tapeline. All macrophyte taxa were recorded on the transects (width 10 m) starting at the willows or forest by the side of the lake and reaching into the water. Their relative abundances on the transects were estimated on a modified Braun-Blanquet scale (semi-quantitative estimation): 1 – single plant or a few plants; 2 – scattered plants or some small stands; 3 – numerous, frequent in the observation area; 4 – dominant or co-dominant; 5 – mass occurrence, absolute dominant. The abundance of macroscopic filamentous green algae for every station was estimated according to the same scale (0–5), but separately from submerged macrophytes due to their different life/growth form. Littoral water transparency (SD) was measured from a boat in the deepest part of the studied transects.

Epiphytic algae and littoral phytoplankton were studied in parallel, at the same ten stations in 2005–2015. The amount of epiphytic algae was studied on the basis of chlorophyll *a* (Chl*a*) content on the dominating macrophytes: common reed (*Phragmites australis*) in the emergent belt; perfoliate pondweed (*Potamogeton perfoliatus*) and spiked milfoil (*Myriophyllum spicatum*) among submerged species. Additionally, in 2012–2015 epiphytic biomass was calculated for comparison with the air-dry weight (ADW = air-dry biomass) of these plant species. The amount of epiphytes was calculated for the mass unit of the dried and weighed host plant. The dominating genera of epiphytic algae were studied in the same sample, preserved with formaldehyde solution,

and counted using the Utermöhl (1958) method. This method allowed us to distinguish the other algal groups apart from the dominating diatoms: cyanobacteria (planktonic species with gas vacuoles not taken into account), chlorophytes, and others.

The samples of littoral plankton were taken from among reed stands or from above thick beds of submerged plants using a bottle. They were treated as pelagic phytoplankton: preserved with Lugol's (acidified iodine) solution and studied using the Utermöhl (1958) method.

2.4. Data used for the calculations of total biomasses

For the estimations of ADW of macrophytes, epiphyton, and phytoplankton, we used published data sets (Mäemets and Freiberg, 2004; Mäemets et al., 2006), reports of the Estonian State Monitoring Programme, and unpublished data sets of the authors, shortly introduced below.

In 1999–2002, a SCUBA diver conducted sampling of submerged plants at 10 stations; two 0.5 m × 0.5 m replicates were taken when plants occurred. This timespan included the highest spring WL in 1999, and the lowest level for these sampling years in spring in 2000 (see Fig. 2). We incorporated the annual ADW averages for *Potamogeton perfoliatus*, *P. pectinatus*, and filamentous green algae of these two years as extremes at maximum and minimum WLs (Table 2) into calculations of total hypothetical ADW. Total biomass of epiphytes (see Subsection 2.5) on *P. perfoliatus* (Table 2) was calculated using the extreme values of the host plant.

The biomass of the epiphytes on *Phragmites* was calculated for ADW of the submerged biomass of *Phragmites*. It was based on the overall mean shoot length and air-dry biomass in the lake: 2.6 m and 1000 g m⁻², respectively. These mean values were based

Table 2. Values used for the calculations of average air-dry weight (ADW) of macrophyte shoots, epiphytes, and phytoplankton (littoral + pelagial) and the years of sampling

Producer	Average ADW		
	at max water level	at min water level	Overall
<i>Phragmites australis</i> shoots, g m ⁻²			1000
<i>Potamogeton perfoliatus</i> shoots, g m ⁻²	23.3 (1999)	48.4 (2000)	
<i>Potamogeton pectinatus</i> shoots, g m ⁻²	0.8 (1999)	4.6 (2000)	
Epiphytes on <i>Phragmites</i> , mg g ⁻¹	–	–	0.55
Epiphytes on <i>P. perfoliatus</i> , mg g ⁻¹	–	–	1.96
Phytoplankton in northern part in August, g m ⁻³	0.68 (2010)	2.52 (2006)	
Phytoplankton in southern part in August, g m ⁻³	2.16 (2010)	8.70 (2006)	
Large filamentous algae, g m ⁻²	0	18.5 (2000)	

– Not measured.

on 79 samples collected in 2001–2002 and 69 samples collected in 2012. The extreme averages of the depth limit for *Phragmites australis* were 0.2 m in 2006 (minimum) and 1.3 m in 2010 (maximum), which accounted for 8% and 50% of the mean shoot length, respectively. We considered their ratio 8% : 50% \approx 1 : 6 as the proportion of the biomass inhabited by epiphytes at the extreme WLs. For the sake of simplicity, when calculating the submerged part at the highest WL, we divided the 90 m \times 1 m reed belt into three 30 m sub-zones with the following proportion of the submerged part: 8% (20 cm submerged), 19% (50 cm), and 50% (130 cm). In these three zones the submerged part of reed weighed 80, 190, and 500 g m⁻², respectively.

The values of phytoplankton ADW in August, the month of maximum FBM in the lake, were calculated for the whole lake, not separately for the littoral and the pelagial (Table 2). For the biomass of phytoplankton at the lake volume 28.91 km³ we used the FBM in 2010, and at the volume 21.57 km³, the FBM in 2006, according to the volume percentages of the lake parts and averages of FBM in the northern and southern parts. The ADW was calculated as 20% of the wet biomass and was used for comparison with the ADW of submerged plants and algae. The wet biomass of phytoplankton was compared with values in Table 3, for estimation of the ecological status for Peipsi (order document No. 44 by Estonian Minister of Environment).

2.5. Statistics

The relationships between the characteristics of pelagic water and WL were tested for two different lake parts using a generalized linear model (SAS/STAT GENMOD), where the effect of the locations of the sampling stations and seasonality (month) were included. The water variables were log-transformed to meet the assumption of normality. The change in macrophyte abundance and reed width related to the change in the WL was tested by Spearman correlation analysis and a generalized linear model. Correlations were tested at significance level 0.01 using the sum of the relative abundances of species in 10 stations per year ($n = 11$). The generalized linear model with repeated measures for the sampling sites ($n = 110$) was used to estimate the effect of WL on macrophyte abundance. The Poisson distribution was used for macrophyte abundances and the dispersion parameter was estimated by Pearson's chi-square statistic divided by its degrees of freedom.

3. RESULTS

3.1. Water-level related changes in the pelagial

Significant relationships (Table 4) between the characteristics of pelagic water and WL in 1997–2015 were found for the majority of the analysed variables mentioned

Table 3. Values of phytoplankton (wet) biomass (FBM) and abundance of large filamentous green algae used for the assessment of the ecological status of Lake Peipsi according to the Water Framework Directive (adapted from order document No. 44 by Estonian Minister of Environment: Pinnaveekogumite..., 2009)

Indicator	Lake part	High	Good	Moderate	Poor	Bad
FBM (April–October), mg/L	Peipsi <i>s.s.</i>	≤ 1	(1–2.6]	(2.6–9.4]	(9.4–17.3]	>17.3
	Lämmijärv and Pihkva	≤ 2.6	(2.6–6.4]	(6.4–16.1]	(16.1–37]	>37
Abundance of large algae 1–5	Whole lake	0	1	2–3	4	5

Table 4. Estimated change with confidence limits of pelagic water characteristics at 1 m decrease of water level for two parts of Lake Peipsi according to the monthly samples of May–August 1997–2015. n – number of samples; FBM – phytoplankton biomass; CNR – water colour; DIN – dissolved inorganic nitrogen; TP – total phosphorus; PO4P – phosphates; SD – Secchi depth

Variable	Peipsi <i>s.s.</i> ($n = 282$)		Lämmijärv ($n = 115$)	
	Estimated ratio	p -value	Estimated ratio	p -value
FBM	1.2 (1.01–1.5)	0.0475	1.7 (1.4–2.2)	<.0001
CNR	2.0 (1.8–2.2)	<.0001	1.8 (1.6–2.1)	<.0001
DIN	1.2 (1.0–1.5)	0.0423	1.8 (1.3–2.6)	0.0012
TP			0.8 (0.7–1.01)	0.0125
PO4P	1.3 (1.0–1.6)	0.0173	1.6 (1.1–2.3)	0.0271
SD			1.2 (1.1–1.4)	0.0017

in Section 2.2. In the northern, largest part (Peipsi *s.s.*) the water colour (CNR), the content of dissolved inorganic nitrogen (DIN), and phosphates (PO₄P) were positively related to WL. The same correlations were found for the shallow and steadily more dark-watered (Table 1) southern part (Lämmijärv), but there also the rise in the FBM at the low WL was more pronounced. Remarkably, for this lake part also a positive correlation between water transparency (SD) and WL and a negative correlation of total phosphorus (TP) with WL were found (Table 4).

Our study period included extreme values of WL: close to the absolute minimum (see Section 2.1) in 2003, 2006–2007, and 2014–2015, and close to the absolute maximum in 1999 and 2010–2011 (see Fig. 2). Comparison of the data of these two groups for the whole lake revealed that the average CNR (°) in May–August of the high-water years (mean ± SE): 81.9 ± 3.01 ($n = 68$) was more than two times as high as in the years of the lowest WL: 36.4 ± 1.42 ($n = 128$). Remarkably, this increase of the CNR was not connected with a significant increase in the chemical oxygen demand by dichromatic consumption (CODCr) at high WL ($34.2 \pm 1.42 \text{ mg O L}^{-1}$) and at low WL ($30.6 \pm 0.84 \text{ mg O L}^{-1}$). At low water, the CNR value was about 1.6 times lower than the mean CNR and positively correlated with CODCr ($r = 0.5$, $p < 0.0001$) and FBM ($r = 0.5$, $p < 0.001$). The correlation between CODCr and FBM was significant at low ($r = 0.56$, $p < 0.001$) as well as at high WL ($r = 0.33$, $p = 0.008$). The relative importance of phytoplankton carbon in TOC (see Section 2) increased with the decreasing WL (Fig. 4).

Comparison of SD between the littoral and the pelagial for 2005–2015 showed its lower values at sampling time in the littoral: $0.96 \pm 0.04 \text{ m}$ versus $1.25 \pm 0.05 \text{ m}$ in the pelagial (t -test $p < 0.001$, $n = 69$). Similarly to the pelgial of the shallow Lämmijärv, the SD of the littoral had a positive correlation with the WL ($r = 0.29$, $p = 0.012$).

3.2. Relations of macrophytes and large filamentous algae with water level in 2005–2015

The abundance (summarized over the stations) of several macrophyte species increased appreciably at low WLs (Fig. 5). Large filamentous green algae *Cladophora* (dominant), *Spirogyra*, *Mougeotia*, *Ulothrix*, *Chaetophora*, *Zygnema*, etc. were markedly supported by low WLs ($r = -0.71$). Besides the increase in the total species number (including shore plants and helophytes) at the retreating water, the number of submerged species was also significantly ($r = -0.82$) higher at low WLs. Shallow water in spring was the most favourable for *Potamogeton perfoliatus* ($r = -0.81$), *Myriophyllum spicatum* ($r = -0.76$), *Potamogeton pectinatus* ($r = -0.74$), and *Chara contraria* A. Braun ($r = -0.65$). Results of modelling predicted a 1.6–4-time increase in the abundance of these species at a 1 m decrease in the WL (Table 5). Moreover, low water was favourable for two rare, protected species: amphibious *Alisma gramineum* Lej. ($r = -0.53$) and hygrophilous *Cyperus fuscus* L. Nutrient-demanding *Lemna gibba* L. and *Zannichellia palustris* L. occurred more frequently at low WLs. Despite high temperatures at high WLs in

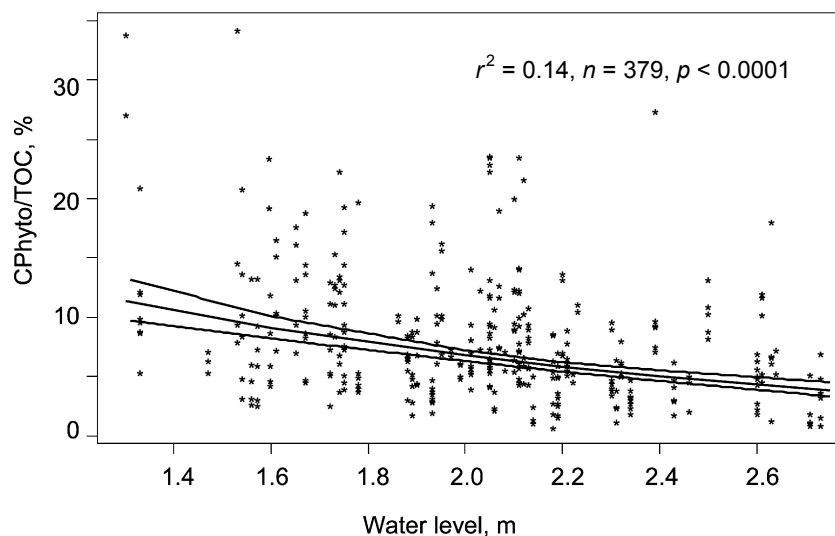


Fig. 4. Percentage of the carbon content in phytoplankton (CPhyto) in the total organic carbon (TOC) in Lake Peipsi in May–August 1997–2015, predicted mean with 95% confidence limits.

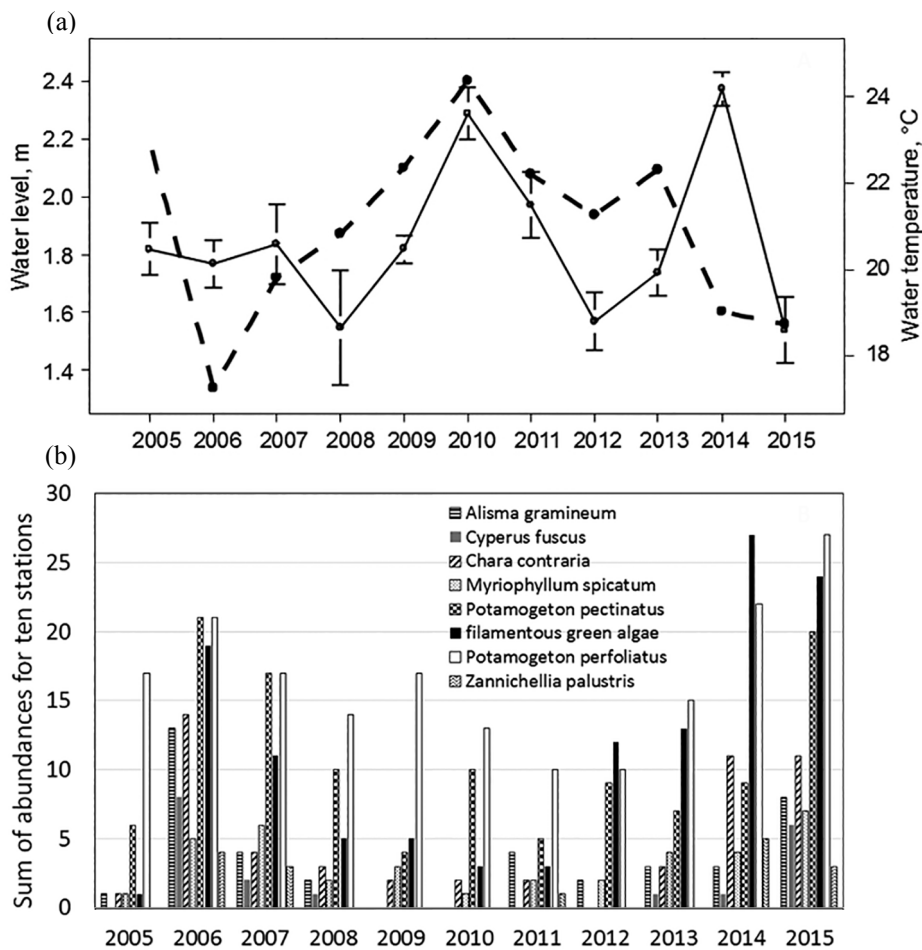


Fig. 5. Summertime (July–August) water level of Lake Peipsi, temperature, and occurrence of taxa that showed a significantly different abundance between the years: (a) summer water level (dashed line) and water temperature (continuous line); (b) summarized abundance estimates for every year, all 10 stations together. Life forms: submerged: *Chara*, *Potamogeton*, *Myriophyllum*, *Zannichellia*; amphibious: *Alisma*; hygrophilous: *Cyperus*.

Table 5. Results of generalized linear modelling (GENMOD): estimated increase with confidence limits of abundance at a 1 m decrease in the mean water level of Lake Peipsi; $n = 100$

Variable	Estimated ratio (confidence limits)	p -value
Number of submerged species	2 (1.6–2.6)	0.007
Total number of species on transect	1.6 (1.3–2)	0.003
<i>Potamogeton perfoliatus</i>	1.6 (1.1–2.1)	0.03
<i>Potamogeton pectinatus</i>	2.5 (1.5–4)	0.026
<i>Myriophyllum spicatum</i>	3.4 (1.7–6)	0.01
<i>Chara contraria</i>	4 (1.6–10)	0.038
Large filamentous green algae	3.1 (1.7–5)	0.014

2010 (Fig. 5a), the occurrence of any of the aforementioned taxa was not enhanced.

Most reliable data on *Phragmites* were obtained at the measurements of a narrow stand on the northern shore, not affected by cutting unlike the stands on the north-west shore. In the southern stations reed stands were wider (100 m or more) and of a changeable shape, not allowing accurate measurements. The stand of

Phragmites studied on the northern coast was exposed to the longest fetches of the lake and its mean depth limit was 0.3 m. The width of the stand displayed appreciable oscillations (Fig. 6), but was not significantly correlated with the WL. In the southern part of the lake, where the depth limit of reed was mostly >1 m, we observed tangled and yellowing reed at rising WLs.

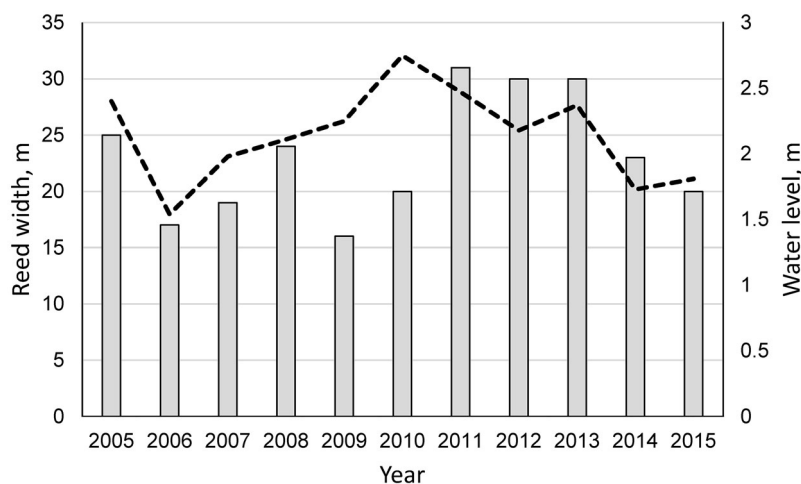


Fig. 6. Width of the reed belt at Rannapungerja (northern coast of Lake Peipsi) and water level (dashed line, average of May–July).

3.3. Water level and epiphyton

The growing depth of reeds in sampling places of EP was 0.2–1.7 m (for 90% 0.2–0.6 m) and that of submerged plants 0.1–3.5 m (for 90% 0.2–1.9 m). Calculated to the ADW of the host plant, the amount of EP was the highest on *Myriophyllum* and the lowest on *Phragmites* (Table 6). The amount of EP according to Chl_a showed a weak negative correlation with the growing depth of the host plant (all host species taken together). The strongest of these correlations was found for *Potamogeton* ($r = -0.37$, $p < 0.001$; Fig. 7), followed by *Phragmites* ($r = -0.18$, $p = 0.046$), but it was lacking for *Myriophyllum*. Although most of the diatoms were identified to the genus level and only larger diatoms to the species level, it was possible to distinguish an average of 30 diatom taxa per sample. The percentage of diatoms in the EP on *Potamogeton* increased in direct

proportion to the growing depth of the host plant, at the expense of attached forms. At the same time, the percentage of predominantly metaphytic (not attached) chlorophytes and the total number of species decreased with depth. Irrespective of this relationship, a low WL per se did not cause an increase of EP. In fact, high Chl_a values for EP were found on *Phragmites* and even higher values on *Myriophyllum* in 2010, at the highest WL and the highest temperature (see Fig. 5a).

3.4. Littoral and pelagic phytoplankton

Extremely large FBM values were caused by the accumulation of colonies of cyanobacteria (CY) on the leeward side. When such wind-induced peaks (water blooms visible with the naked eye) were excluded from the calculations, littoral phytoplankton was characterized by yearly fluctuations, which were quite similar to the

Table 6. Descriptive statistics on main results for littoral phytoplankton and epiphyton Chl_a, 2005–2015; epiphyton biomass 2012–2015. Abbreviations: FBM – phytoplankton biomass, CY – cyanobacteria, BAC – diatoms, CHL – chlorophytes, bm – biomass, Chl_a – chlorophyll *a*, EP – epiphyton

Variable	Unit	Valid <i>n</i>	Mean	Lower quartile	Upper quartile	SD	SE
FBM littoral	mg L ⁻¹	110	9.25	3.73	8.28	13.4	0.77
CY bm littoral	mg L ⁻¹	110	6.08	1.50	5.40	13.1	0.75
BAC bm littoral	mg L ⁻¹	110	2.31	0.58	2.64	3.0	0.17
CHL bm littoral	mg L ⁻¹	110	0.58	0.35	0.65	0.4	0.03
Chl _a EP <i>Myriophyllum</i>	µg g ⁻¹	36	84.00	45.60	110.11	60.4	8.77
Chl _a EP <i>Phragmites</i>	µg g ⁻¹	118	13.00	6.66	16.07	10.7	0.98
Chl _a EP <i>Potamogeton</i>	µg g ⁻¹	157	50.44	23.00	64.06	37.3	2.97
EP bm <i>Myriophyllum</i>	mg g ⁻¹	20	2.88	1.40	3.59	2.39	0.54
EP bm <i>Phragmites</i>	mg g ⁻¹	52	0.55	0.20	0.48	1.38	0.19
EP bm <i>Potamogeton</i>	mg g ⁻¹	65	1.96	1.13	2.53	1.25	0.16

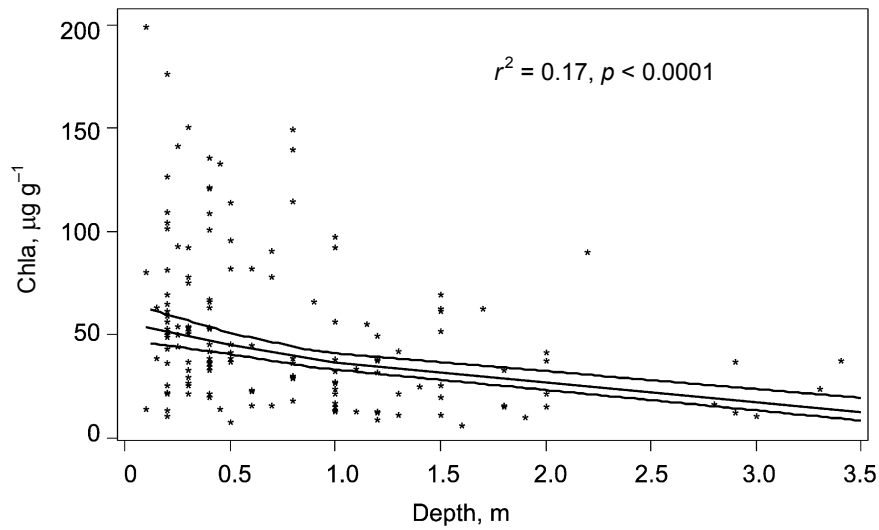


Fig. 7. The amount of epiphytic Chla on *Potamogeton perfoliatus* at different depths in July–August 2005–2015 in Lake Peipsi, predicted mean with 95% confidence limits.

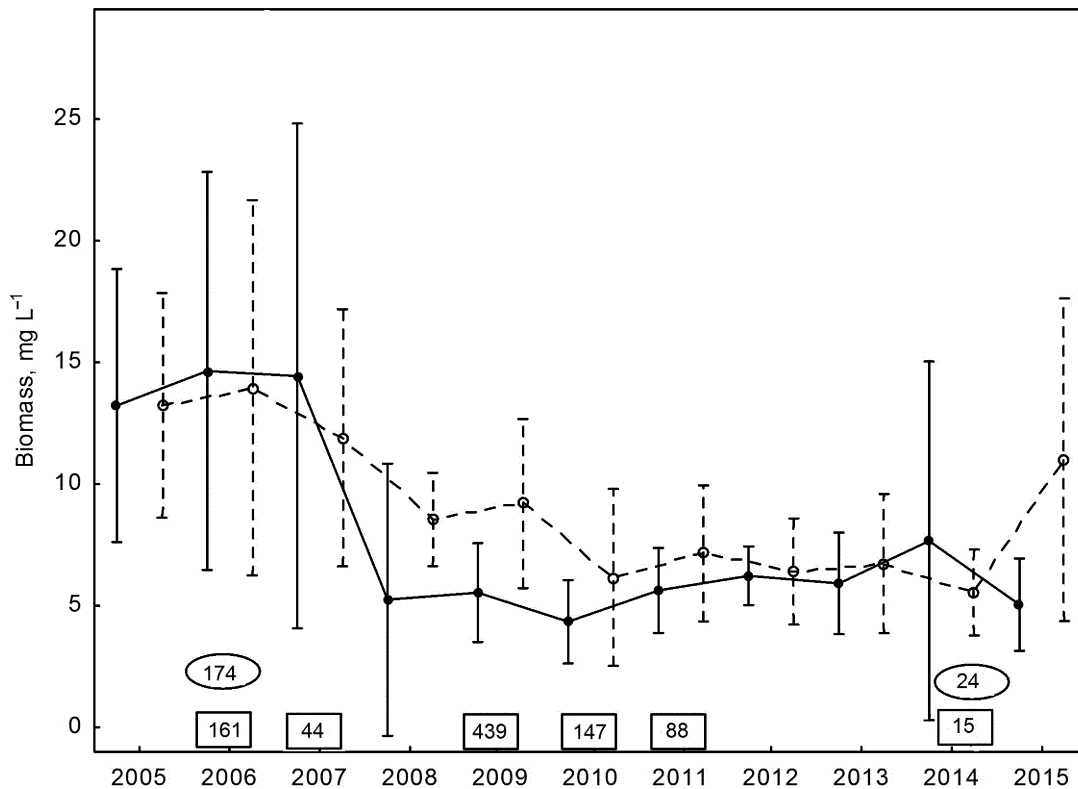


Fig. 8. Phytoplankton biomass in the littoral and pelagic areas of Lake Peipsi in different years. The biomass values of the cyanobacterium genera higher than 15 mg L^{-3} are not presented on the graph but at the bottom of the graph: ellipse – *Anabaena*; rectangle – *Gloeotrichia*. $n = 110$.

dynamics of the pelagic phytoplankton in 2005–2015 (Fig. 8), but somewhat richer in species, especially regarding CY and chlorophytes. The genera *Microcystis*, *Aphanizomenon*, and *Anabaena* (*Dolichospermum*) as

well as *Gloeotrichia echinulata* (J. E. Smith) P. Richter constituted the main part of the littoral phytoplankton in summer, either simultaneously or intermittently. In the course of the 11 years of littoral study, macroscopic

colonies of *G. echinulata* accumulated at 1–4 stations in six years, and mass colonies of the genus *Anabaena*, in the years 2006 and 2014, after the lowest spring WL (Figs 2 and 8).

The influence of WL on the FBM and on other water quality characteristics was stronger in the shallow southern part, Lämmijärv (Table 4). In 2005–2015, some phytoplankton components (CY and chlorophytes) and total FBM displayed an inverse correlation with the WL in summer, both in the pelagial ($r = -0.16$, $p < 0.006$) and in the littoral ($r = -0.24$, $p = 0.016$).

3.5. Differences in primary producers at extreme water levels and assessment of ecological status

To estimate the magnitude of WL-related biomass changes, we calculated the extremes of ADW for the dominating species and/or groups of producers (Table 7), based on the data in Table 2. The calculation of the ADW of the submerged reed shoots at high WLs yielded 23.1 kg per a 1 m wide transect of the 90 m reed belt. For the lowest WL, the ADW of submerged reed was calculated as 1/6 of the submerged reed at the highest WL, and it was about 3.7 kg for the transect.

In Lake Peipsi the phytoplankton ADW dominated over the ADW of submerged plants and epiphytes (Table 7). Interestingly, the ratios of biomasses at the lowest to the highest water level were similar: 2.2 for *Potamogeton* spp. and 2.6 for phytoplankton. Regarding the FBM (mean \pm SE for growing period), the ecological status of Peipsi according to the Water Framework Directive (order document No. 44 by Estonian Minister of Environment) was estimated for Lämmijärv as ‘Poor’ in 2006 (18.6 ± 3.0 mg/L) and ‘Moderate’ in 2010 (7.6 ± 1.2 mg/L) and for Peipsi *s.s.* ‘Moderate’ in 2006 (7.1 ± 0.8 mg/L) and ‘Good’ in 2010 (2.5 ± 0.3 mg/L). Moreover, considering the high abundance of large green algae in 2006 and their absence in 2010, the status of the northern lake part was ‘Poor’ or ‘High’, respectively. The differences in the amounts of these algae were analogous to the years 2000 and 1999 (Tables 2 and 7).

4. DISCUSSION

4.1. Effect of the fluctuating water level on the food web

In Lake Peipsi, the pelagic area is considerably larger than the littoral area, and phytoplankton biomass exceeds to a significant degree that of submerged macrophytes (but not *Phragmites*). Our results reveal that independently of the prevailing group, the difference of the ADWs of these two submerged producers at extreme WLs may be similar. However, it is probable that in boreal lakes of lower trophic levels the extreme ADW differs within a lesser amplitude. In Peipsi, the twofold difference in easily degradable biomass (algae and/or submerged plants) must have a significant influence on the heterotrophic part of the food web. Our results are in accordance with the statements that WLF cause shifts between the clear and turbid state independently of the anthropogenic nutrient enrichment and top-down effects (Coops et al., 2003; Scheffer and Van Nes, 2007; Bakker and Hilt, 2016). Moreover, it seems that in the large fluctuating shallow lakes the food web is governed by the WL via resuspension, turbidity, and productivity. The recent studies in Peipsi showed an increase in the internal phosphorus loading with the lowering of the WL; the CY biomass in August positively correlated with this loading (Tammeorg et al., 2016). A low WL creates favourable conditions for sediment resuspension, which results in reduced water transparency due to increased concentrations of suspended solids and phytoplankton. Increased resuspension and phosphorus loading at low WLs were found also in the large, extremely shallow Lake Võrtsjärv (Nõges and Nõges, 1998). Moreover, in Võrtsjärv surface water temperature and WL explained approximately half of the total variability in water parameters (total P, total N, Secchi depth, biological oxygen demand) commonly used in the ecological status assessment of lakes (Nõges and Tuvikene, 2012).

Despite the decline of transparency at low WLs, we cannot exclude the favourable effect of low spring floods (Fig. 2), because the water of Peipsi is the clearest in spring, until June. Keddy (2010) suggested that larger

Table 7. Biomass of the main primary producers in Lake Peipsi at extreme water levels (WL), calculated on the basis of minimum/maximum values of air-dry weight (ADW). For macrophytes were used extreme ADW values in 1999–2002, for phytoplankton in 2005–2015. The used values are presented in Table 2

Producer	ADW (t) at min WL	ADW (t) at max WL
Submerged part of <i>Phragmites</i> shoots, available for epiphyton	1 932	12 063
Epiphytes on <i>Phragmites</i>	1.1	6.6
Shoots of <i>Potamogeton perfoliatus</i> + <i>P. pectinatus</i>	530	241
Epiphytes on <i>Potamogeton perfoliatus</i>	1.2	0.5
Large green algae (calculated only for 20 m belt)	185	≈ 0
Phytoplankton of the whole lake (pelagial + littoral) in August	69 065	26 156

temperature fluctuations and light pulses at low WLs, especially in spring, stimulate the germination of propagules. Similarly, Lombardo (2005) highlighted the importance of spring light conditions. Light favours significantly the germination of *Chara* oospores, since it activates cytochromes (Takatori and Imahori, 1971). During the period of our study, the best year for *Ch. contraria* was 2006, when the WL was very low already in spring (Figs 2 and 5). According to Van Nes et al. (2002), even a short clear-water phase can have a significant effect on charophyte dominance.

Because of the synergistic effects of environmental influences, the impact of a specific individual factor cannot be identified in every case. In earlier studies on Peipsi (Milius et al., 2005; Haldna et al., 2008) it seemed that nutrients were mostly influenced by the WL, while the FBM (particularly of CY) was also influenced by the water temperature. Besides the WL, extraordinary weather conditions may also trigger long-term shifts in the plankton community in the following seasons. A steep decline in the pelagic FBM in 2008 followed the ice-free winter of that year. That winter modified significantly the balance of nutrients and the phenology of phyto- and zooplankton in Peipsi (Blank et al., 2009).

In large lakes, the inertia of processes may be stronger and the impact of not only temperature but also of the WL may be more delayed than in smaller water bodies (cf. Beaulieu et al., 2013). The amount and composition of littoral phytoplankton depend to a large extent on the prevalent direction of the wind at the sampling, and the dominants may change within a very short time. We had an opportunity to follow this situation in the littoral at the Kodavere station in July 2010 where *G. echinulata* was absent at the time of sampling but became a dominant within two hours. The biomass of phytoplankton in the wind-exposed littoral may be about ten times as high as in open water owing to the presence of this macroscopic cyanobacterium.

Also freezing, desiccation, and abrasion may have a greater influence at low WLs. Some seeds need mechanical or chemical treatment (Dubyna et al., 1993; Preston and Croft, 1997). The drying stimulates seed germination (de Winton et al., 2004) probably due to a change in the redox status (Kalin and Smith, 2007). For the reeds, the impacts of other, more accidental factors, e.g. the direction of the wind at the time of ice run, freezing of the rhizomes, etc., may overcome the effect of WLF. Sometimes large torn fragments of reed stands drift around.

Regarding the epiphytes, our hypothesis that a low WL would enhance their growth was not verified. The effect of the WL on EP was somewhat ambiguous, while the effect of the wind and waves, in conjunction with the effect of the growing depth of the host plant

on its biomass and composition, appeared to be more important. Furthermore, whereas EP peaks were found at the lowest (2006) as well as at the highest WLs (2010), the long-lasting high temperature apparently overcame the negative impact of the high WL in 2010. In Peipsi a decrease in EP with increasing depth may be explained by the fact that the percentage of non-attached chlorophytes decreased with depth. Hence, the impact of the WL was moderated by mechanical stress. The amount of EP in relation to the growing depth varied mostly on *Potamogeton* and least on *Phragmites*. The reason is that the range of the variability of the latter's growing depth was narrower.

4.2. Allochthonous and autochthonous organic matter

According to Wantzen et al. (2008), the flood phase (high-water period) facilitates the deposition and temporal storage of organic matter in the aquatic–terrestrial transition zones of lakes. On the other hand, Larmola et al. (2004) found that a shorter and weaker spring flood could increase the amount of organic matter remaining in the upper shore zones, thus promoting a higher net release of CO₂ during a longer post-flood period. Due to the sheer size of Peipsi and the strong mechanical stress there, the storage of organic matter may take place in different ways. In the shore side part of wide reeds, particles of organic remains may be retained, but in the open area they may be washed away to the surf zone. Their deposition depends on the bottom topography, size of particles, etc. However, the inflow of allochthonous organic matter takes place mainly at high water, and an intense aeration and the mineralization of all organic matter prevail at low WLs. The decomposition and mineralization at retreating WLs promote a new rise in the phytoplankton and macrophyte production in the lake. Wantzen et al. (2008) emphasize also wave action, breaking the litter, and the impact of frost in northern temperate lakes at low WLs.

The 'brownification' (cf. Granéli, 2012; Kritzberg and Ekström, 2012) of Peipsi seems to be a periodic WL-driven fluctuation. The rising of CNR but not CODCr at high WLs is probably due to the refractory character of allochthonous organic matter in comparison with autochthonous organic matter. Recalling Wetzel (1992), decomposition of DOM from wetland and littoral areas is slow. In comparison, FBM had a positive correlation with CODCr at different WLs, but the relative importance of phytoplankton in TOC increased during the years of the minimum WL, reflecting the rise in autochthonous organic matter. Obviously, the decomposition of inflowing humic compounds needs further investigation. The positive correlation between the

content of DIN and the WL may reflect a higher inflow from the surroundings (Kangur et al., 2003), but also a less intensive use at the decline in the abundance of the producers in the lake at high WLs.

4.3. Two-pronged effects of water level oscillations

Our results suggest that in low-water periods takes place internal nutrient enrichment from sediments and by decaying remains of lake producers. This amplifies cyanobacterial blooms, considered as a clear indicator of eutrophication (Stroom and Kardinaal, 2016). Using the abundance of this group as an indicator for the estimation of ecological status yields differences between the low- and high-water years. Also large green algae (phytobenthos), considered good indicators in the lakes under hydrological pressures and with an altered WL, as well as for local hot spots of stressors around the lake (Kelly et al., 2016 and references therein), are more abundant at low WLs and cause poorer estimation of the ecological status. Effects of seasonality and naturally changing WL overshadow the effects of anthropogenic stress on nutrients, Chla, FBMs, and SD in Võrtsjärv (Tuvikene, 2018). Low water is favourable for nutrient-demanding hydrophytes such as *Lemna gibba* and *Zannichellia palustris*. On the contrary, low water enhances macrophytes, which are indicative of a good status. In temporary habitats available due to retreating water, species declining due to eutrophication and the overgrowing littoral (*Cyperus fuscus* and *Alisma gramineum*) occur. An increase in submerged species and in total species richness – indicators of a good status – also took place at low WLs. Thus, the estimations of lake status according to different groups of biota may yield different results.

Our results support the theory that species richness is the highest at the intermediate disturbance (Connell, 1978). Also Wantzen et al. (2008) emphasized that floodpulse represents an intermediate disturbance and supports maximum species richness. A low WL has a positive impact on macrophyte species richness, but concurrently it enhances overgrowth of shallow slopes by tall plants (reeds) and ‘centrifugal’ distribution of species: tall productive plants occupy the main, largest part of the habitat and small plants (incl. *Alisma* and *Cyperus*) are pushed to peripheral areas (Keddy, 2010). The effect of high-water years on reeds seems to have also a two-pronged effect. In our study the reed stand in the shallowest water was more successful in high-water periods but in initially deeper growth areas reeds declined in these years. According to Vretare et al. (2001), *Phragmites* in deeper waters allocates less resources to its below-ground part and is therefore more sensitive

to uprooting. Rising water reduces the supply rate of oxygen to the submerged parts by increasing the path to the rhizomes (Deegan et al., 2007).

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Primaarproduktentide sõltuvus veetaseme kõikumisest Peipsi järves

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Peipsi järve (pindala 3555 km²) veetase on väga muutlik: aasta keskmiste väärtuste erinevus küünib 1,5 meetrini. Veetaseme kõikumiste mõju fütoplanktonile, makrofüütidele (suurtaimedele) ja epifüüttonile (taimsele pealiskasvule) uuriti Eesti poole kümnes litoraali seirepunktis aastail 2005–2015 ning kõrvutati ka pelagiaalis samal perioodil uuritud veeproovide andmeid veetaseme muutustega. Selgus, et litoraali ja pelagiaali fütoplanktoni muutused olid samalaadsed, välja arvatud tuule mõjul akumulatsioonivahetavate süanobakterite (sinivetikate) suurem hulk litoraalis veedõitsengute ajal. Võrreldes maksimum- ja miinimumveetasemega aastaid, leiti, et madalaima veeseisu korral suurenesid oluliselt: a) fütoplanktoni biomass ja selle osatähtsus vee orgaanilise süsiniku sisalduses, b) suurtaimede liigirikkus ja biomass, sealhulgas veesiseste taimede ning makrovetikate oma. Epifüütide rohkuses ei ilmnenud veetasemega olulist seost. Madalaim ja kõrgeim vegetatsiooniperioodi veetase erinesid 1 m ning penikeelte biomass oli madalaima veetaseme korral 2,2 ja fütoplanktonil 2,6 korda suurem kui kõrgeima veetaseme korral.

Peipsi järve ökoloogilise seisundi hinnang võib miinimum- ja maksimumveetaseme juures erineda vähemalt ühe kvaliteediklassi võrra. On tähelepanuväärne, et fütoplanktoni ja suurte niitrohevetikate põhjal tehtud järeldused on vastupidised suurtaimede põhjal tehtud otsustele: madala veega suureneb oluliselt fütoplanktoni ja suurte niitrohevetikate biomass (näitavad veekogu kehva seisundit), aga samaaegselt kasvab suurtaimestiku liigirikkus ning veesiseste taimede ja mändvetikate biomass (peetakse hea seisundi tunnusteks).

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