Proceedings of the Estonian Academy of Sciences,
2016, **65**, 4, 394–407
doi: 10.3176/proc.2016.4.07
Available online at www.eap.ee/proceedings

ECOLOGY

Eutrophication-driven spatial and temporal changes in macrophyte diversity in Lake Peipsi

Helle Mäemets[*], Kadi Palmik, and Marina Haldna

Centre for Limnology, Estonian University of Life Sciences, 61117 Rannu, Tartumaa, Estonia

Received 5 January 2016, revised 21 May 2016, accepted 23 May 2016, available online 22 November 2016

Abstract. We examined spatial and temporal changes of the macrophyte species richness in Lake Peipsi by comparing the frequency of 76 taxa in earlier (1970 and 1980; 49 stations) and recent (1997–2014; 52 stations) data sets. About 35% of these taxa appeared or became largely distributed later than 1970. Significant changes in frequency during the study period were observed for 53 taxa. The period of rapid eutrophication since the 1970s coincided with a clear increase in the species number in the southern, recently hypertrophic lake part. Changes in Shannon's diversity index were analogous to the dynamics of species number, but species evenness did not change significantly. Species that appeared and/or increased their frequency after the 1970s were common hygrophytes, helophytes, and amphibious plants inhabiting the overgrowing littoral. A remarkable growth was observed in the frequency of *Phalaris arundinacea*, *Glyceria maxima*, *Sium latifolium*, *Agrostis stolonifera*, and *Rorippa amphibia* while among hydrophytes mainly plants of sheltered habitats such as *Spirodela*, *Hydrocharis*, *Lemna*, *Nuphar*, *Ceratophyllum*, *Sparganium*, *Stratiotes*, and *Elodea* increased their frequency. In repeatedly studied 22 stations filamentous algae, *Potamogeton gramineus*, *P. pectinatus*, and *Stratiotes* had appeared by 1980. In these 22 stations the average species number per year in 1997–2014 was similar to or lower than in 1980, and the total average had decreased. Using cluster analyses of 243 observations in 52 stations, six contemporary characteristic littoral vegetation types for L. Peipsi were identified, among them species-rich small landing places and wide monodominant reeds. Our results indicate that anthropogenic eutrophication increased the species number of macrophytes at its beginning, but in L. Peipsi the hump-backed curve is not clearly expressed. The number of species in the lake stays stable due to large oscillations in the water level, removal of reeds, and cleaning of boat canals.

Key words: macrophytes, species richness, eutrophication, sheltered habitats.

1. INTRODUCTION

The decrease in biodiversity is a worldwide anthropogenic process and declines appear to be far greater in fresh waters than in most affected terrestrial ecosystems (Sala et al., 2000; Jenkins, 2003). However, this process in fresh water is less studied. In the terrestrial habitats of the temperate zone many plant species become rare due to widely distributed fertilized agricultural areas, forest clearance, urban landscapes, and biological invasions. Moreover, grassland experiments in the Netherlands involving addition of phosphorus and nitrogen doubled the biomass production but decreased the species diversity by 50% (Willems et al., 1993). Also litter production increases at fertilizing, hindering seed germination (Berendse and Aerts, 1994; Foster and Gross, 1998). All these impacts may be accompanied by eutrophication of water bodies, causing large-scale changes in the temporal patterns and spatial variations in species diversity (e.g. Jupp and Spence, 1977; Sand-Jensen et al., 2008; Mäemets et al., 2010).

The form of species richness–productivity and species richness–disturbance relationships has generated much controversy, myriad models, and few generalizations (Graham and Duda, 2011). The best-known productivity–richness relationship is unimodal or hump-backed: richness

---

[*] Corresponding author, helle.maemets@emu.ee

increases at low to intermediate levels of productivity and decreases at high productivity. This theory has been debated since the 1970s and was summarized for terrestrial vegetation by Rajaniemi (2003): few species can tolerate very low resource levels while greater diversity occurs at intermediate productivity. Productivity is expected to have the greatest impact on diversity when disturbance is of intermediate frequency (Rajaniemi, 2003). The dispute about the role of the resource competition as a vegetation determinant is concluded by Grime (2007): competition declines in importance under the impacts of reduced productivity and/or severe disturbance.

Considering the results on terrestrial plant communities, we can suppose that a high nutrient load may decrease the macrophyte species diversity also in lakes. However, it may strongly depend on the initial conditions of ecosystems. An analysis of producer diversity responses to local manipulations of the resource supply revealed a species richness increase in freshwater systems due to fertilization (Hillebrand et al., 2007). On the contrary, the species number of hydrophytes in Lake Fure (Denmark) decreased with the increasing nutrient load in the lake during its transition from mesotrophy (1911) to eutrophy (1951) and to hypertrophy (1983), and formed about 2/3 of the initial number (37) at the improvement of the state back to eutrophy in 2005 (Sand-Jensen et al., 2008). In that lake the nutrient enrichment stimulated phytoplankton growth and restricted the distribution of small angiosperms, mosses, and characeans by reducing water transparency. Tall angiosperms became dominant while small species vanished. Recolonization of the lost species was considered to be hindered by the rarity of the propagules of declining species, by less consolidated sediments, shading and competition by reeds, tall submerged angiosperms, and fast-growing macroalgae (Sand-Jensen et al., 2008). Conclusions by Alahuhta et al. (2014) that besides submerged species also emergent plants are important in detecting anthropogenic pressures are related to the results by the above-mentioned authors about shading and competition by reeds.

In comparison with terrestrial vegetation, fertilization of water bodies more frequently replaces life forms, not only species. Also invasive species may change the diversity of various macrophyte functional life forms. For example, a highly competitive tropical signal grass has been proved to have a negative effect on helophytes and rooted submersed species, contributing to the decrease in plant diversity (Michelan et al., 2010). According to the centrifugal model (Keddy, 2010), at increased fertility fast-growing tall plants prevail, occupying the major, less-disturbed part of a wetland or lake littoral. Small plants of infertile, open habitats are supported by disturbed, mostly peripheral areas. In the large shallow L. Peipsi an increase in reeds has been the main obvious change of macrophyte vegetation during the last 50 years, causing a decline of species of the open water edge (Mäemets and Freiberg, 2004; Mäemets et al., 2010). Measuring net primary productivity for comparison with species richness, mentioned by Graham and Duda (2011), is less used in such cases, because tall emergent plants are undoubtedly more productive than small hygrophytes, amphibious and submerged plants.

A floristic work (Mäemets et al., 2010) that compared data of all study stations of L. Peipsi until 1980 with all later data from 1997–2007 revealed a significant decrease in the frequency of 20 taxa (among 67 registered for both periods). However, this comparison was generalized for the whole lake and did not include the newest data of L. Pihkva, the southernmost, hypertrophic part of the lake. In 2008–2014, additional floristic data were collected, including also L. Pihkva. Therefore, a new detailed analysis was needed for different lake parts comparing the floristic data from all available data sets since 1970. The main aim of the study was to examine detailed patterns of macrophyte species richness in time and space by analysing floristic changes in different parts of L. Peipsi. We tested the hypothesis that species number increases at the beginning of eutrophication and decreases or stabilizes in the later periods.

2. MATERIAL AND METHODS

2.1. Site description

The total surface area of the transboundary Lake Peipsi is 3555 km^2, mean depth 7.1 m, and maximum depth 15.3 m. The lake consists of three parts: the largest and deepest northern part L. Peipsi *s.s.* (Chudskoe in Russian), the southern part L. Pihkva (Pskov), and the intermediate, river-like L. Lämmijärv (Teploe) (Fig. 1). The average volume of the whole L. Peipsi is 25.07 km^3 and the water residence time is about two years. The water level is unregulated; the amplitude of average annual fluctuation of the water level during the period 1890–2005 was 1.5 m and its absolute range 3 m. Because of this and due to the shallow slope of the lake basin large areas become flooded or denuded, especially in the northern part where a belt of 100 m is habitable for shore plants at the lowest water level. In L. Peipsi, as is common in all temperate zone lakes, the water regime has two low-water (winter and summer) and two high-water (spring and autumn) periods. However, the autumn high water is usually considerably lower than the spring high water (Jaani et al., 2008).

The main part of the lake basin is located on the outcrop of Devonian sandstones, but in the northern part limestone of the Upper Ordovician and in the southernmost tip limestone of the Upper Devonian lie very close (Vaher, 2008). The content of carbonate in the sand and silt decreases southwards (Raukas, 2008). Sand shores prevail, but also till, sandstone cliff, peat,

Fig. 1. Location of study stations: o – stations in 1970 and 1980; * – stations in 1997–2014; the names of 22 stations that are best comparable are underlined.

and clay border the lake. The most complex are the sediments of the river-like L. Lämmijärv where paludification takes place due to the neotectonic movement of the bedrock. There peat spreads in several places besides sandy and clayey sediments. Vegetation is rare or absent in the areas where the bottom consists of loose sand, sandstone, cobble, or boulders and where the shore is under strong mechanical stress caused by fetch and waves. The rhythmical natural change in the water level is a disturbance factor for macrophytes.

The trophy level of L. Peipsi has increased step by step from the mesotrophic–eutrophic state to eutrophic–hypertrophic during decades, depending on the lake part (Starast et al., 2001; Kangur et al., 2002; Kangur and Möls, 2008; Milius and Haldna, 2008; Leeben et al., 2013; Tammeorg et al., 2013). The northern part, L. Peipsi *s.s.*, was mesotrophic until the 1970s (Mäemets et al., 1996) and eutrophic during the last decades. The southernmost part, L. Pihkva, was earlier eutrophic (Kangur et al., 2007) but hypertrophic in the last decades, and L. Lämmijärv displays intermediate characteristics (Kangur et al., 2013).

Table 1. Number of macrophyte taxa of different ecological groups in Lake Peipsi in 1997–2014

Ecological group	Number of taxa
Xerophytes (on dunes, occasionally registered)	33
Mesophytes	22
Hygrophytes, helophytes	125
Amphibious plants	7
Floating-leaved plants	7
Floating plants	7
Submerged plants	32
Macroscopic algae (Chlorophyta mainly on genus level)	17

The vegetation composition of L. Peipsi is described and analysed in several earlier publications (Mäemets and Mäemets, 2000, 2001; Mäemets et al., 2010). The recent taxa list (most on species, some on genus level) of L. Peipsi contains 250 taxa of vascular plants, mosses, and macroscopic algae (Table 1). Earlier lists of 180 species (Sudnitsyna et al., 2008) vs 145 species (Mäemets et al., 2010) were published. These large differences between the numbers of species are mainly due to the unavoidably subjective decisions about including various shore plants, e.g. ruderals of landing places, xerophytes of dunes, willow species, etc.

The dominating *Potamogeton perfoliatus* L. and *Phragmites australis* (Cav.) Trin. ex Steud. have kept their positions in L. Peipsi during the last 50 years. Two most sensitive taxa – *Isoëtes echinospora* Durieu and *Subularia aquatica* L. – have not been found since the 1960s and the 1970s, respectively. Masses of the nutrient-demanding *Lemna gibba* L. were for the first time found in 2006–2007. Other new species found since the 1980s are *Potamogeton praelongus* Wulfen, *P. acutifolius* Link ex Roem. et Schult., *Ceratophyllum submersum* L., *Nitella syncarpa* (Thuillier) Chevallier, and *N. hyalina* (De Candolle) Agardh.

2.2. Data sets

Samples for orthophosphate ion (PO4-P) were analysed at the Institute of Zoology and Botany during 1965–1992 and at the Central Laboratory of the Estonian Environmental Research Centre during 1992–2014. The laboratories applied identical methods (described in detail by Starast et al. (2001)).

In 1970 and 1980 attention was payed to hydrophytes, helophytes, and amphibious plants, but in 1997–2014 shore species were included more completely. For the calculations of the species occurrence in 1970 and 1980

Table 2. Division of investigated stations between different basins of Lake Peipsi

Data set	L. Peipsi *s.s.*	L. Lämmijärv	L. Pihkva
49 stations in 1970 and 1980	22	9	18
52 stations in 1997–2014	26	11	15
22 stations comparable for all times	10	4	8

we used the original unpublished data set by Aime Mäemets and found that 76 taxa were present in all, earlier (1970 and 1980) and recent (1997–2014) data sets; however, in several cases only on genus level. According to the determinations, during the last 19 years *Carex* sp. was represented mainly by *C. acuta* L., and *Chara* sp. by *C. contraria* A. Braun ex Kütz., but small-sized *Juncus* spp. contained at least five species. Undetermined mosses seem to be mostly *Fontinalis antipyretica* f. *gracilis* (Lindb.) Schimp. In parallel to *Eleocharis palustris* (L.) Roem et Schult. and *E. uniglumis* (Link) Schult., also intermediate forms, supposedly their hybrids, were frequent. Our determinations rely on the specimens stored in the Herbarium of the University of Life Sciences – TAA in 1970–2014.

In 1997–2014 all herbaceous species were registered starting on the shore, from the edge of bushes and trees until the visible (from boat) stands of submerged plants (mainly *Potamogeton perfoliatus*). Submerged plants were sampled using a plant hook (as shown in Katanskaya, 1981). In all studies the relative abundance of taxa per station was estimated on a 1–5-point semi-quantitative scale of Braun-Blanquet: 1 – single plant or few plants; 2 – scattered plants or some small stands; 3 – numerous, frequent in the observation area; 4 – dominant or codominant; 5 – mass occurrence, absolute dominant. We emphasize the term *relative* as the scale used was not identical to the coverage scales of Braun-Blanquet or DAFOR but displays the importance of a species in the corresponding group (emergent, submergent, etc.).

The distribution of the stations in the lake parts is presented in Table 2. The 49 stations studied by A. Mäemets in 1970 and in 1980, as well as the 52 stations studied by us in 1997–2014, were located more or less regularly along the whole coast. Among all old and new stations 22 were the same in 1970, 1980, and 1997–2014 (Fig. 1).

2.3. Statistical methods

Data on PO4-P and water transparency (Secchi depth, SD) from May to October 1965–2015 were used to illustrate eutrophication processes in L. Peipsi. From the Russian side, samples for 1992–2002 were absent, but using the multiparametric linear model approach (Haldna et al., 2013), the predictions with the confidence interval were estimated separately for L. Peipsi *s.s.* and its southern part (L. Lämmijärv and L. Pihkva) every year and every lake part.

For assessing differences in the species diversity between the different lake parts and time periods, the number of species, Shannon's diversity, and Pielou's evenness were estimated and tested using ANOVA (Oksanen et al., 2012).

Nonparametric multivariate analysis of variance using permutation tests for distance matrix (Bray–Curtis dissimilarity measures on the basis of species abundances) was used to estimate the temporal effect of phosphates and water transparency on the species community (PERMANOVA using R package vegan (R Core Team, 2013; Oksanen et al., 2012).

Data sets of the 49 old and 52 new stations were used for the calculations of the average species number per station and for species frequencies per station at different times. This means that the number of stations where a species was found was divided by the total number (Table 2) of the studied stations. The species frequency and the significance of its change were found for the whole lake and separately for the three lake parts. We tested differences in the proportion of each species in 1970 (marked I), 1980 (II), and in 1997–2014 (III) using the z-test (Freund and Wilson, 2003).

The data set of 52 new stations with a repeated survey during 1997–2014 (243 observations) was used to analyse vegetation types. Cluster analysis with Euclidean distance and Ward's method (Ward, 1963) based on the abundance of macrophyte species was used to clarify the source of variability. To determine the appropriate number of clusters, a plot of the total within-groups sum of squares against the number of clusters was used (Hothorn and Everitt, 2014). The resulting clusters were characterized as contemporary main habitat/vegetation types with characteristic species. Their indicator species were found on the basis of species abundances for different clusters. Group-equalized *IndVal.g* was used as the association index (De Cáceres et al., 2010). Species with the association value (indicator value) ≥0.4 were selected. All calculations were carried out using statistical package R.3.1.1 (R Core Team, 2013).

3. RESULTS

3.1. Indicators of eutrophication

Among the indicators of eutrophication earlier data were available for PO4-P and water transparency. A rapid increase in the PO4-P content occurred in 1970 (Fig. 2a), then it started to decrease and was the lowest in the high-water period of 1985–1990. During the last decades we could not reveal any clear trend in the PO4-P content of the water. A continuous decrease of Secchi depth can be observed in the whole lake (Fig. 2b).

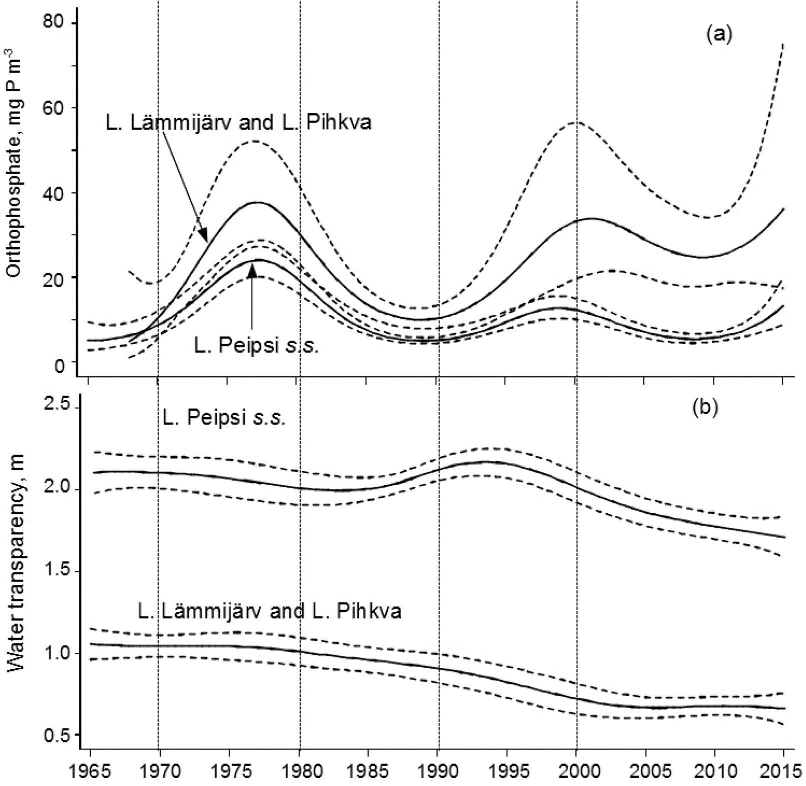

Fig. 2. Predicted mean values with 95% confidence limits of summer ortophosphate concentrations (a) and water transparency (b) in L. Lämmijärv, L. Pihkva, and L. Peipsi *s.s.*

3.2. Changes in species number and diversity

In the northern part of L. Peipsi the average number of macrophyte species per station did not largely change during the last decades (Fig. 3a). In 1970 (I) this lake part (L. Peipsi *s.s.*) was the richest in species. However, between 1970 and 1980 in the southern parts of the lake a remarkable increase in the species number, exceeding the values in L. Peipsi *s.s.*, took place. Between 1980 (II) and the latest period (1997–2014, III) changes in the species richness for the lake parts were contradictory: in L. Peipsi *s.s.* and in L. Lämmijärv the number of species slightly decreased but in L. Pihkva a small increase occurred. Changes in Shannon's diversity were analogous to the dynamics of species number (Fig. 3b). Although there have been remarkable changes in the species numbers, species evenness displayed only a slight, insignificant decline in the southern lake parts (Fig. 3c).

About 2/3 of the compared 76 taxa appeared or became largely distributed in study stations after 1970 (Table 3). A significant change for the whole lake occurred in the frequency of 53 vascular taxa and of the group of filamentous green algae. The main increase took place in the frequency of common hygrophytes, helophytes, and amphibious plants inhabiting overgrowing shores. Alongside the already dominating *Phragmites*, a remarkable increase was observed in the frequency of *Phalaris arundinacea*, *Glyceria maxima*, *Sium latifolium*, *Agrostis stolonifera*, and *Rorippa amphibia*. It is notable that among the hydrophytes mainly the frequency of the plants of sheltered habitats, such as S*pirodela*, *Hydrocharis*, *Lemna*, *Nuphar*, *Ceratophyllum*, *Sparganium*, *Stratiotes*, and *Elodea* increased (Table 3). Compared to the taxa lists in 1970, in the latest lists the proportion of helophytes increased from 55% to 70% and the share of amphibious plants decreased from 11.3% to 3.9%. In the latest period, lemnids temporarily appeared also in the open water: *Lemna trisulca* along the whole western coast in 1999 and masses of *Lemna gibba* between Gdovka (on the eastern shore, Fig. 1) and the opposite shore in 2006–2009.

Significant changes by lake parts are shown in Appendix A, comparing the study times I–III, I–II, II–III. The highest number of species with a changed frequency was observed in L. Pihkva.

Comparison of L. Peipsi *s.s.* and L. Pihkva revealed the following floristic peculiarities in the course of the last 40 years:

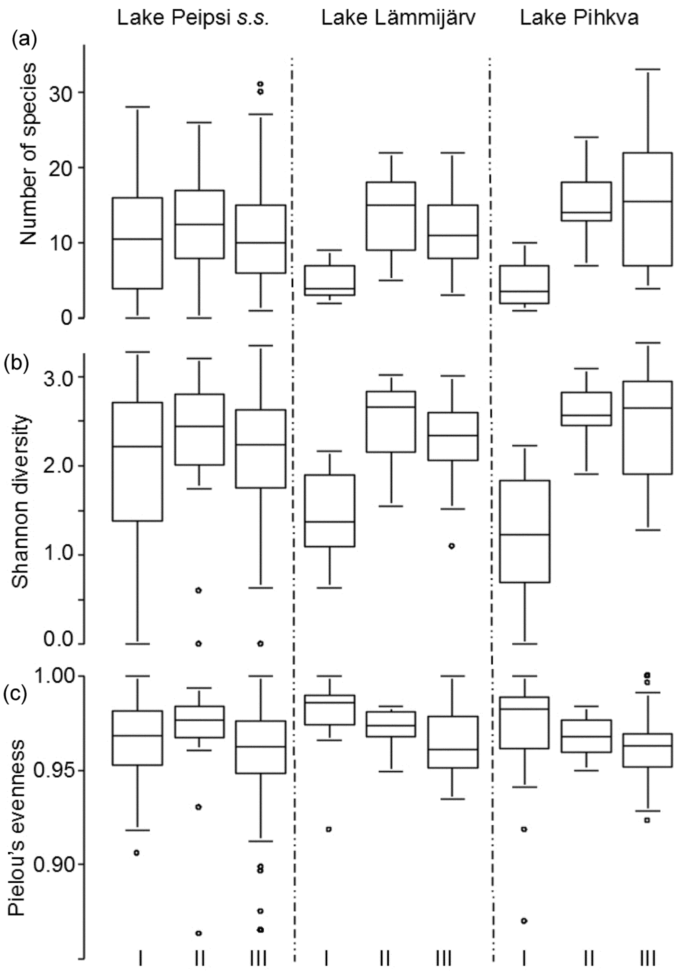

Fig. 3. Average number of macrophyte species per station in different lake parts at different study times (a), Shannon diversity index (b), and Pielou's evenness (c). Boxplots indicate median values and interquartile ranges while whiskers show 5% and 95% quantiles. The Roman numbers: I – 1970; II – 1980; III – 1997–2014.

L. Peipsi *s.s.*

- Main area for *Chara* (*contraria*), *Alisma gramineum*, and rare narrow-leaved *Potamogeton* species;
- Only this lake part saw a significant increase in the frequency of *Phragmites* (and appearance of *Solanum dulcamara*) between 1970 and the present;
- The latest increase in the frequency of *Carex acuta* and *Typha latifolia.*

L. Pihkva (the highest trophy level during the whole period of investigations)

- Main area for the increase of nymphaeids and lemnids;
- Main area for *Typha angustifolia*, *Oenanthe aquatica*, *Stratiotes aloides.*

According to the results (see Appendix A), the eutrophication of L. Peipsi moved towards the northern part of the lake and was accompanied with an increase in the species number of macrophytes. The majority of the new species are nowadays common inhabitants of the water edge. The results of PERMANOVA indicated a statistically significant ($p = 0.001$) effect of sampling site, year, phosphates, and water transparency on the species community in different time periods, supporting the hypothesis that plants followed changes in the trophic state.

The 22 best-comparable stations around the lake (Fig. 1) demonstrated that the largest change took place between the years 1970 and 1980, when the species number increased at least twofold in 14 stations (Table 4). This increase was supported mainly by the following species: *Butomus umbellatus*, *Polygonum amphibium*, *Rumex hydrolapathum*, *Alisma plantago-aquatica*, *Carex* spp., *Glyceria maxima*, *Sagittaria sagittifolia*, and *Equisetum fluviatile.* Moreover, at the increasing trophy level in 1980 several hydrophytes such as *Potamogeton pectinatus*, *Potamogeton gramineus*, *Stratiotes aloides* and large filamentous algae appeared. Among all studied stations the most remarkable change took place at the station Spitsyno (L. Peipsi *s.s.*), where the species number increased from 0 to 19 within a period of 11 years (1970–1980). Then in this station scarce stands of *Schoenoplectus lacustris* formed and abundant *Butomus umbellatus*, *Eleocharis acicularis*, *Ranunculus reptans*, filamentous algae, *Potamogeton gramineus*, *P. pectinatus*, *Chara* sp., and *Alisma*

Table 3. Macrophyte taxa and their functional groups appearing or revealing significant (z-test) changes in frequency (*F*). A – amphibious; S – submerged; FL – floating; FLL – floating-leaved; I – isoetids; H – helophytes and hygrophytes

Taxon	Growth forms	*F* in 1970	*F* in 1980	*F* in 1997–2014
Appeared/disappeared*				
Ceratophyllum demersum L.	S	2	0	48
Fontinalis antipyretica Hedw.	S	2	0	35
Hydrocharis morsus-ranae L.	FL	0	12	37
Glyceria fluitans (L.) R. Br.	H	0	0	12
Iris pseudacorus L.	H	0	18	21
Lysimachia vulgaris L.	H	0	12	38
L. thyrsiflora L.	H	0	6	23
Lythrum salicaria L.	H	0	24	52
Mentha arvensis L.	H	2	0	31
Myriophyllum verticillatum L.	S	0	0	19
Nymphaea sp.	FLL	0	4	13
Oenanthe aquatica (L.) Poir.	H	0	0	25
Phalaris arundinacea L.	H	0	6	63
Potamogeton crispus L.	S	0	0	8
P. obtusifolius Mert. et W. D. J. Koch	S	0	0	2
Ranunculus lingua L.	H	0	2	12
Scirpus radicans Schkuhr	H	0	2	19
Solanum dulcamara L.	H	0	2	19
Sparganium erectum s.l.	H	0	8	27
Subularia aquatica L.	I	8	2	0
Utricularia australis & *vulgaris*	S	0	0	6
Significant change in frequency				
Acorus calamus L.	H	4	20	23
Alisma gramineum Lej.	A	29	47	54
Elatine hydropiper L.	A	2	4	17
Nuphar lutea (L.) Sm.	FLL	4	16	37
Phragmites australis	H	76	84	96
Potamogeton pectinatus L.	S	33	51	73
Sagittaria sagittifolia L.	A	35	59	65
Scolochloa festucacea (Willd.) Link	H	2	6	23
Sparganium emersum Rehmann	FLL	2	10	29
Typha angustifolia L.	H	4	14	21
Butomus umbellatus L.	H	18	61	73
Eleocharis acicularis L.	A	12	47	65
Equisetum fluviatile L.	H	10	39	48
Glyceria maxima (Hartm.) Holmb.	H	8	35	56
LARGE FILAMENTOUS ALGAE		16	49	69
Lemna trisulca L.	FL	2	24	42
Polygonum amphibium L.	A	12	53	46
Agrostis stolonifera L.	H	16	6	81
Alisma plantago-aquatica L.	H	12	31	67
Eleocharis palustris	H	27	29	71
Elodea canadensis Michx.	S	8	16	48
Juncus spp.	H	8	4	56
Lemna minor L.	F	2	10	33
Myosotis scorpioides L.	H	4	8	52
Myriophyllum spicatum L.	S	12	10	56
Rorippa amphibia (L.) Besser	A	2	10	67
Rumex maritimus L.	H	4	2	44
Spirodela polyrhiza (L.) Schleid.	F	2	14	37
Stratiotes aloides L.	S	2	14	44
Typha latifolia L.	H	6	4	33
Carex sp. (supposedly *acuta* L.)	H	14	43	73
Sium latifolium L.	H	12	47	75
Rumex hydrolapathum Huds.	H	4	35	10

---

* Appeared/disappeared taxa include only the species of our study stations.

Table 4. Number of macrophyte species in the same stations at different study times

Stations	1970	1980	Average per year in 1997–2014	Total in 1997–2014 (and observation times)
Lake Peipsi *s.s.*				
Rannapungerja	8	9	5.5	26 (11)
Tammispää	22	26	11.9	39 (14)
Raja	13	13	11.5	36 (13)
Lahepera	14	24	13.3	46 (12)
Varnja	8	22	10	41 (14)
Zigoska-Vetvennik	2	16	3.3	10 (4)
Kunest	3	9	11.3	22 (3)
Spitsyno	0	19	17	35 (5)
Raskopel	18	17	8.3	22 (4)
Podlip'e	14	18	17.4	34 (5)
Average	10.2	17.3	11	
Lake Lämmijärv				
Meerapalu	4	7	12	20 (2)
Mehikoorma	9	22	14.3	31 (4)
Räpina	4	14	11.7	31 (10)
Kobylje-Zhelcha	7	19	9	24 (4)
Average	6	15.5	11.8	
Lake Pihkva				
Lüübnitsa	7	14	7.7	12 (3)
Värska	9	16	23.7*	49 (11)
Pupkovo-Baglitsy	8	24	24**	41 (3)
Orlovo-Meshokol	7	21	20.5**	44 (4)
Molgino-Zidilov Bor	3	13	14.7	29 (3)
Vidovitshi	5	14	15.7	33 (3)
Zimni Borok-Litovitchi	5	16	11.7	21 (3)
Budovitchi-Piusa	3	11	9.5	17 (2)
Average	5.9	16.1	15.9	
Total average for 22 stations	7.9	16.5	12.9	

* Including species of sedge meadow.
** Cleaned boat canals.

gramineum appeared. The increase in the species number did not continue up to the latest period. Although the total number of macrophyte species in the repeatedly visited stations was high in 1997–2014, the average number per year was similar or lower in comparison with the species number in 1980, and the total average for 22 stations had decreased (Table 4).

3.3. Main types of macrophyte vegetation in 1997–2014

The observed significant impact of sampling sites on the species composition inspired us to distinguish types of lake vegetation. Using abundance estimations of macrophyte taxa, 243 observations (at 52 stations in 1997–2014) were divided into six clusters, representing main types of vegetation in parallel with the geological conditions in the relevant area (Table 5). *Phragmites australis* and *Potamogeton perfoliatus* were the dominating taxa in the whole lake except for some parts of L. Pihkva where *Typha angustifolia* and *Nuphar lutea* prevailed. Among 80 macrophyte taxa 40 were associated with only one cluster and were regarded as indicators. However, for clusters 1–5 the species with the indicative value >0.4 are shown, but in the station of Värska Bay the indicative value >0.7 was used (Table 5). The reason was that 23 indicator species were revealed there due to a large number of specific marsh species. All observations in Värska Bay formed **cluster 6**, the richest in species.

The next two richest in species, although floristically very different, were clusters 1 and 2. **Cluster 1** contains mainly observations in boat canals, at river mouths, and at the south-western shore of L. Pihkva, where mighty stands of *Typha angustifolia* form labyrinths.

Table 5. Characteristics of the main lake habitat types in 1997–2014 according clustering on the basis of floristic composition

	Clusters					
	1	2	3	4	5	6
No. of observations	32	46	46	75	33	11
Lake part*	P L S	P L S	P L S	P L S	P L S	P (Värska Bay)
No. of observations	15 8 9	10 2 34	9 2 35	4 24 47	5 1 27	11
Shore type, ordered by importance	Sand, till, clay, peat	Sand, till, clay, boulders	Sand, till, boulders	Sand, till clay, peat, boulders	Sand, till	Sand
Average and range of species No.	21 (6–57)	20 (7–41)	7 (3–16)	18 (3–55)	14 (7–26)	34 (26–41)
Average and range of species No. of hydrophytes	7 (1–15)	5.5 (2–13)	3.7 (1–11)	2.9 (0–17)	5.2 (3–10)	6.4 (2–12)
General description of the habitat	Boat canals, river mouths, helophyte mazes	Reed stands & open shore stretches	Shallow water occupied by helophytes	Gaps in shore reeds or stretches of strong wind stress	Reed stands & open shore stretches	Bay and its flooded meadow
Indicators**	*Spirodela* *Hydrocharis* *Ceratophyllum dem.* *Lemna trisulca* *Sparganium erectum s.l.*	*Potamogeton gramin.*	Indicators absent	*Calystegia* *Petasites* *Sonchus arvensis* *Eupatorium*	Large filam. algae *Chara contraria*	*Caltha* *Comarum* *Calamagrostis canesc.* *Lathyrus pal.* *Typha ang.* *Nuphar lutea* *Lysimachia thyrsiflora* *Equisetum fluviatile* *Stratiotes* *Carex acuta*

---

* Lake parts: P – L. Pihkva; L – L. Lämmijärv; S – L. Peipsi *s.s.*

** The names of indicative species are shortened to the genus when only one species was present in the flora.

The vegetation of **cluster 2** is characteristic of shore stretches with fragmentary reeds providing open areas at the water edge and in shallow water. This cluster includes many observations at the partially reed-free shores of landing or swimming places (indicator species *Potamogeton gramineus*). This habitat type shares many of the species with other clusters and is probably the most typical representative of the macrophyte flora of L. Peipsi. Thus, clusters 2 and 5 shared *Alisma gramineum*; clusters 1, 2, and 5 *Butomus umbellatus*; clusters 1, 2, 4, and 5 *Agrostis stolonifera*, *Eleocharis uniglumis*, *Rumex maritimus*, and *Juncus* spp. **Cluster 5** is closely related to cluster 2, representing also a combination of reed and open areas, but observations differ in time (see below). The poorest in species, **cluster 3,** represents inaccessible water edges caused by high water and/or wide thick reeds, or shores where the suitable zone for macrophytes was very narrow. On the contrary, at observations in **cluster 4** the water edge was easily accessible but under a strong mechanical stress, hindering the growth of the rooted hydrophytes. In the narrow river-like L. Lämmijärv the scarcity of hydrophytes was probably caused by the bottom conditions or currents. Indicative were shore species growing in sparse reeds between willows and the lake.

Repeated observations at the same stations occurred in different clusters in several cases. The number of annually studied stations was too small for the statistical verification of the impact of water level on species occurrence. However, in parallel with a constant floristic composition in half of 10 Estonian annually (2005–2014) monitored stations, observations in three to four stations belonged to cluster 5 in the years of the lowest water. Cluster combinations for Estonian monitoring stations are shown in Appendix B. Relevance to cluster 5 at the lowest water in 2006–2007 and in 2014 was remarkable for the stations located in the shallow-sloped north-western part of the lake (stations Raja and Tammispää).

4. DISCUSSION

Our results support the hypothesis that the nutrient enrichment of L. Peipsi caused considerable changes in the species richness of macrophytes. The use of the hump-backed curve (Graham and Duda, 2011) may be more or less acceptable when supposing that it is peaked now, without a clear decrease at the recent trophic state of the lake. Considering the curve of orthophosphate ion (Fig. 2a), there seems to be a retardation of eutrophication. One possible explanation of this questionable slowing down may be the formation of new habitats, able to retain large amounts of nutrients.

Macrophytes are important quality elements for ecological assessments and many species have been listed as either eutrophication sensitive or tolerant (Penning et al., 2008). Occurrence of *Isoëtes echinospora* Durieu and *Subularia aquatica* L. in L. Peipsi *s.s.* in the 1960s (Tuvikene, 1966; Nedospasova, 1974) reflects the prevailing of open littoral lacking common hydrophytes. In parallel with the increasing anthropogenic load expanding overgrowing of shallow water with medium-sized or large fast-growing plants and lemnids and disappearance of sensitive species occurred. Meaningfully, these new habitats present increasing heterogeneity of vegetation and are more or less separated from the open lake. Similar habitat changes were described by Andersson (2001), who detected the appearance of *Lemna minor* and *Glyceria maxima* in sheltered bays of Lake Vättern with ongoing eutrophication and the formation of denser stands of littoral vegetation. Also Alahuhta et al. (2012) found that *G. maxima* and other helophytes respond to changes in nutrients.

The increase in littoral vegetation/habitat types may be the reason why it is impossible to compare our results with the data on more or less homogeneous vegetation types, e.g. largely studied grasslands (Adler et al., 2011; Fraser et al., 2015). Very probably, the littoral as an ecotone must be divided into zones for such comparisons. Adler et al. (2011) stated that the hump-shaped pattern has emerged most frequently in studies that cross community boundaries – as in the case of our recent study. Besides changes in the macrophyte species composition, nutrient enrichment is known to contribute to the proliferation of filamentous algae (Dodds and Gudder, 1992). The same pattern was described in L. Peipsi where the frequency of large filamentous algae increased considerably in the course of the rapid eutrophication in the 1970s.

When discussing the reliability of our results the question about the occurrence of species by chance at the single-year observations (in 1970 and 1980) arises. It is at least partially answered by the average species numbers of the same 22 stations during all investigation times. In these stations the increase in the species number did not continue until the latest period (1997–2014): the average species number per year was similar or lower in comparison with 1980, and the total average species number had decreased.

Another question is connected with the fact that the naturally changing water level of L. Peipsi is an important temporal disturbance factor. In low-water summers the denuded zone, especially in the north-western shore, provides a wide wet ecotone – a habitat for small-sized hygrophytes, helophytes, and amphibious plants. Van Geest et al. (2005a, 2005b, 2007) clearly showed that lakes with partial drawdown reveal a significantly higher species richness of submerged macrophytes than lakes with no drawdown. However, the average water level in 1980 was 33 cm higher than the average in 1970. Consequently, the higher macrophyte species number in 1980 was not caused by a low-water year. Nevertheless, our annual studies in 2005–2015 confirmed that natural oscillations in the water level support the persistence of species richness at an increasing trophy level, providing peripheral habitats (Keddy, 2010) for declining species. It may be the reason why some rare plants of the open littoral such as *Alisma gramineum* and *Cyperus fuscus* can persist also at overgrowing shores. However, besides the support by water fluctuations they seem to need also human activity (Palmik et al., 2013).

Our present results are somewhat in disagreement with earlier conclusions (Mäemets et al., 2010). For example, species such as *Glyceria fluitans*, *Alisma gramineum*, *Sagittaria sagittifolia*, *Scolochloa festucacea*, *Sparaganium emersum*, *Typha angustifolia*, *Butomus umbellatus*, *Equisetum fluviatile*, *Polygonum amphibium*, *Eleocharis palustris*, *Sium latifolium*, and *Acorus calamus*, which were considered as declining species according to our previous calculations, do not reveal such pattern according to the latest data set used here. The main reason may lie in the more complete data: during the joint transboundary expeditions in the years 2008, 2011, and 2013, we had the opportunity to visit more Russian monitoring stations in L. Pihkva, in which many of the aforementioned species are frequent or even have their main growth areas. Moreover, another reason could be the difference in the numbers of stations and higher relative importance of every station for the calculations of frequency in the present work: 87/139 stations for 1970–1980/1997–2007 in the earlier work versus 49/52 stations for 1970–1980/1997–2014 in the present work.

However, the statement about floristic impoverishment due to thickening reeds is in force, because most species with improved frequency are abundant in new or cleaned canals, which were frequent in the recently visited southern lake part. There an important factor for species richness is human activity. In many places it is impossible to get on the lake, and several study transects were located at small landing places. Therefore our data about average species numbers may be slightly over-estimated. At a high trophy level the shores in the natural condition may be much poorer in species than the shores under moderate human impact, i.e. moderate disturbance. Our results on L. Peipsi suggest that in large lakes with variable habitats the total macrophyte species number, diversity, and evenness may persist or even increase with the nutrient enrichment and their indicative value is low. Water level oscillations and temporary anthropogenic clearances may support a rich flora for a longer time than expected according to the unimodal model.

To estimate the ecological status of a lake on the basis of macrophyte species number and composition needs a discussion about what good status means. The formed new habitats are not characteristic of reference conditions. A larger species number due to the formation of sheltered areas means unfavourable conditions for the declining part of the biota, e.g. suppression of small plants and accumulation of mud on the spawning areas of fish. Sheltered areas provide growing places for invasive species. *Glyceria maxima*, considered invasive in North America, Australia, and New Zealand (Wei and Chow-Fraser, 2006; USDA-NRCS, 2009), becomes abundant at the eutrophication also in its native distribution area (references above, personal communication by the late I. Raspopov in 2007 about L. Ladoga), and *Elodea canadensis* grows mainly in muddy boat canals of L. Peipsi. On the other hand, these areas may provide a valuable habitat for a rich invertebrate fauna, including protected species, therefore possibly increasing functional diversity.

Concluding the results, besides species richness also changes in abundance are important as abundance has been regarded as a much more sensitive indicator of eutrophication (Kolada et al., 2011). Considering the extent of the areas under the vegetation of types 1 and 3, the state of L. Peipsi is worse than according to the general species richness. Consequently, for the large shallow lakes the estimation of status according to the areas of different habitats may be more justified than the general species richness analysed here.

ACKNOWLEDGEMENTS

Special thanks go to M. Melnik, D. Sudnitsyna, and K. Kozyreva for joint expeditions and data exchange. The authors would like to thank K. Kangur for helpful comments and E. Jaigma for linguistic revision. The study was supported by the Estonian State Monitoring Programme and by the materials of TAA.

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

APPENDIX A

Significant changes in species frequency analysed separately for lake parts (P – L. Pihkva; L – L. Lämmijärv; S – L. Peipsi *s.s.*) over different periods (I –1970, II – 1980, III –1997–2014)

Species	I–III	I–II	II–III	Species	I–III	I–II	II–III
Phragmites australis	S			*Lysimachia thyrsiflora*	S		
Glyceria maxima	P, L, S			*Rumex hydrolapathum*		P	L
Agrostis stolonifera	P, L, S		P, L, S	*Oenanthe aquatica*	P		P
Eleocharis acicularis	P, S	P		*Phalaris arundinacea*	P, L, S		P, L, S
Eleocharis palustris	P		P, S	*Rumex maritimus*	P, S		S
Carex sp.	P, L, S		S	*Scirpus radicans*	P		
Typha angustifolia	P			*Polygonum amphibium*		P	P
Typha latifolia	P		S	*Nuphar lutea*	P		
Juncus sp.	P, S		P, S	*Nymphaea* sp.	P		
Alisma plantago-aquatica	P, L, S		P, S	*Sparganium emersum*	P		
Sagittaria sagittifolia	P	P		*Lemna minor*	S		
Sparganium erectum	P, S			*Lemna trisulca*	P, S	P	
Butomus umbellatus	P, L, S	P		*Spirodela polyrhiza*	P		P
Ranunculus reptans	P			*Hydrocharis morsus-ranae*	P, S		P
Equisetum fluviatile	P	P, L		*Myriophyllum spicatum*	P		P, S
Sium latifolium	P, L, S	P	L, S	*Elodea canadensis*	P		S
Solanum dulcamara	S		S	*Stratiotes aloides*	P		P
Lythrum salicaria	P, L, S	S	P	*Potamogeton gramineus*	P		
Mentha arvensis	S		S	*Potamogeton pectinatus*	P, L	P	
Rorippa amphibia	P, L, S		P, L, S	*Ceratophyllum demersum*	P, L, S		P, L, S
Myosotis palustris	P, S		P, S	*Elatine hydropiper*	P		
Lysimachia vulgaris	P, S			FILAMENTOUS ALGAE	P, S		

APPENDIX B

Floristic relevance of monitoring stations to clusters in different years

Station	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Värska	6	6	6	6	6	6	6	6	6	6
Raigla	4	4	4	4	4	4	4	4	4	4
Laaksaare	*	4	4	4	4	4	4	*	4	4
Pedaspää	3	3	3	3	1	3	3	3	3	1
Varnja	3	3	3	3	3	3	3	3	3	3
Lahepera	*	5	5	2	4	2	2	2	2	2
Kodavere	*	5	3	2	3	3	3	3	3	5
Raja	3	5	5	4	4	4	4	4	4	5
Tammispää	2	5	5	2	2	5	3	5	5	5
Rannapungerja	4	4	4	4	4	4	4	4	4	4

---

* Number of species was too small for cluster analysis.

REFERENCES

Adler, P. B., Seabloom, E. W., Borer, E. T., Hillebrand, H., Hautier, Y., Hector, A., et al. 2011. Productivity is a poor predictor of plant species richness. *Science*, **333**, 1750–1753.

Alahuhta, J., Kanninen, A. & Vuori, K.-M. 2012. Response of macrophyte communities and status metrics to natural gradients and land use in boreal lakes. *Aquat. Bot.*, **103**, 106–114.

Alahuhta, J., Kanninen, A., Hellsten, S., Vuori, K.-M., Kuoppala, M., and Hämäläinen, H. 2014. Variable response of functional macrophyte groups to lake characteristics, land use, and space: implications for bioassessment. *Hydrobiologia*, **737**, 201–214.

Andersson, B. 2001. Macrophyte development and habitat characteristics in Sweden's large akes. *AMBIO*, **30**(8), 503–513.

Berendse, F. and Aerts, R. 1994. Nitrogen-use efficiency: A biologically meaningful definition? *Funct. Ecol.*, **1**, 293–296.

De Cáceres, M., Legendre, P., and Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos*, **119**(10), 1674–1684.

Dodds, W. K. and Gudder, D. A. 1992. The ecology of *Cladophora*. *J. Phycol.*, **28**, 415–427.

Foster, B. L. and Gross, K. L. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, **71**, 2593–2602.

Fraser, L. H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., et al. 2015. Worldwide evidence of a unimodal relationship between plant productivity and species richness. *Science*, **349**, 302–305.

Freund, J. F. and Wilson, W. J. 2003. *Statistical Methods.* Academic Press, USA.

Graham, J. H. and Duda, J. J. 2011. The humpbacked species richness-curve: a contingent rule for community ecology. *Int. J. Ecol.*, **2011**, article ID 868426.

Grime, J. P. 2007. Plant strategy theories: a comment on Craine (2005). *J. Ecol.*, **95**, 227–230.

Haldna, M., Möls, T., Buhvestova, O., and Kangur, K. 2013. Predictive model for phosphorus in the large shallow Lake Peipsi: approach based on covariance structures. *Aquat. Ecosyst. Health Manag.*, **16**(2), 222−226.

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E., Cleland, E. E., Elser, J. J., et al. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc. Natl. Acad. Sci. USA*, **104**,10904–10909.

Hothorn, T. and Everitt, B. S. 2014. *A Handbook of Statistical Analyses Using R*. Third Edition. CRC Press, Boca Raton, FL.

Jaani, A., Klaus, L., Pärn, O., Raudsepp, U., Zadonskaja, O., Gronskaja, T., and Solntsev, V. 2008. Hüdroloogia [Hydrology]. In *Peipsi* (Timm, T., Raukas, A., and Haberman, J., eds), pp. 113–155. Eesti Loodusfoto, Tartu (in Estonian).

Jenkins, M. 2003. Prospects for biodiversity. *Science*, **302**, 1175–1177.

Jupp, B. P. and Spence, D. H. N. 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven: I. Effects of phytoplankton. *J. Ecol*., **65**, 175–186.

Kangur, K. and Möls, T. 2008. Changes in spatial distribution of phosphorus and nitrogen in the large north-temperate lowland Lake Peipsi (Estonia/Russia). *Hydrobiologia*, **599**, 31–39.

Kangur, K., Milius, A., Möls, T., Laugaste, R., and Haberman, J. 2002. Lake Peipsi: changes in nutrient elements and plankton communities in the last decade. *Aquat. Ecosyst. Health Manag*., **5**(3), 363–377

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, 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**(2), 376–387.

Katanskaya, V. M. 1981. *Vysshaya vodnaya rastitel′nost′ kontinental′nykh vodoemov SSSR*. Leningrad.

Kolada, A., Hellsten, S., Søndergaard, M., Mjelde, M., Dudley, B., van Geest, G., et al. 2011. Report of the most suitable lake macrophyte based assesment methods for impacts of eutrophication and water level fluctuations. Deliverable D3.2-3 of the Wiser project.

Keddy, P. A. 2010. *Wetland Ecology. Principles and Conservation*. Second edition. Cambridge University Press.

Leeben, A., Freiber, R., Tõnno, I., Kõiv, T., Alliksaar, T., and Heinsalu, A. 2013. A comparison of the palaeolimnology of Peipsi and Võrtsjärv: connected shallow lakes in north-eastern Europe for the twentieth century, especially in relation to eutrophication progression and water-level fluctuations. *Hydrobiologia*, **710**, 227–240.

Mäemets, H. and Freiberg, L. 2004. Characteristics of reeds on Lake Peipsi and the floristic consequences of their expansion. *Limnologica*, **34**, 83–89.

Mäemets, H. and Mäemets, A. 2000. Commented list of macrophyte taxa of Lake Peipsi. *Proc. Estonian Acad. Sci. Biol. Ecol*., **49**, 136–154.

Mäemets, H. and Mäemets, A. 2001. Macrophytes. In *Lake Peipsi. III. Flora and Fauna* (Haberman, J. and Pihu, E., eds), pp. 9–22. Sulemees Publishers, Tartu.

Mäemets, A., Timm, M., and Nõges, T. 1996. Zooplankton of Lake Peipsi-Pihkva in 1909–1987. *Hydrobiologia*, **338**, 105–112.

Mäemets, H., Palmik, K., Haldna, M., Sudnitsyna, D., and Melnik, M. 2010. Eutrophication and macrophyte species richness in the large shallow North-European Lake Peipsi. *Aquat. Bot*., **92**, 273–280.

Michelan, T. S., Thomaz, S. M., Mormul, R. P., and Carvalho, P. 2010. Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. Freshwater Biol., **55,** 1315–1326.

Milius, A. and Haldna, M. 2008. Hüdrokeemia [Hydrochemistry]. In *Peipsi* (Haberman, J., Timm, T., and Raukas, A., eds), pp. 157–178. Eesti Loodusfoto, Tartu (in Estonian).

Nedospasova, G. V. 1974. Vysshaya vodnaya rastitel′nost′ Pskovsko-Csudskogo vodoema [Higher water vegetation of Lake Pskov-Peipsi]. *Izvestiya GosNIORKh*, **83**, 26–32 (in Russian).

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., et al. 2012. vegan: Community Ecology Package. R package version 2.0-2. 2011.

Palmik, K., Mäemets, H., Haldna, M., and Kangur, K. 2013. A comparative study of macrophyte species richness in differently managed shore stretches of Lake Peipsi. *Limnologica*, **43**, 245–253.

Penning, W. E., Dudley, B., Mjelde, M., Hellsten, S., Hanganu, J., Kolada, A., et al. 2008. Using aquatic macrophyte community indices to define the ecological status of European lakes. *Aquat. Ecol*., **42**, 253–264.

Rajaniemi, T. K. 2003. Explaining productivity–diversity relationships in plants. *Oikos*, **101**, 449–457.

Raukas, A. 2008. Peipsi nõo pinnakatte koostisest ja setete vanusest [On the composition of the Quaternary cover and age of deposits in the depression of Lake Peipsi]. In *Peipsi* (Timm, T., Raukas, A., and Haberman, J., eds), pp. 33–41. Loodusfoto, Tartu (in Estonian).

R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (accessed 2016-09-26).

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. 2000. Global biodiversity scenarios for the year 2100. *Science's Compass*, **287**, 1770–1774.

Sand-Jensen, K., Lagergaard Pedersen, N., Thorsgaard, I., Moeslund, B., Borum, J., and Brodersen, K. P. 2008. 100 years of vegetation decline and recovery in Lake Fure, Denmark. *J. Ecol*., **96**, 260–271.

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.

Sudnitsyna, D. N., Mel′nik, M. M., and Mäemets, H. 2008. Flora Pskovsko-Chudskogo ozera [Flora of Lake Peipsi]. *Vestnik Pskovskogo Gosudarstvennogo Pedagogicheskogo Universiteta*, **6**, 23–57 (in Russian).

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.

Tuvikene, H. 1966. O vysshej vodnoi rastitel′nosti Chudsko-Pskovskogo ozera [Macrophyte vegetation of Lake Peipsi-Pihkva]. *Hydrobiological Researches 4*, 75–79. Tallinn (in Russian).

USDA-NRCS. 2009. The PLANTS Database. Baton Rouge, USA: National Plant Data Center. http:// plants.usda.gov/ (accessed 2016-05-09).

Vaher, R. 2008. Tektoonika [Tectonics]. In *Peipsi* (Timm, T., Raukas, A., Haberman, J., eds), pp. 21–24. Loodusfoto, Tartu (in Estonian).

Van Geest, G. J., Coops, H., Roijackers, M. M., Buijse, A. D., and Scheffer, M. 2005a. Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes. *J. Appl. Ecol*., **42**, 251–260.

Van Geest, G. J., Wolters, H., Roozen, F. C. J. M., Coops, H., Roijackers, R. M. M., Buijse, A. D., and Scheffer, M. 2005b. Water-level fluctuations affect macrophyte richness in floodplain lakes. *Hydrobiologia*, **539**, 239–248.

Van Geest, G. J., Coops, H., Scheffer, M., and Van Nes, E. H. 2007. Long transients near the ghost of a stable state in eutrophic shallow lakes with fluctuating water levels. *Ecosystems*, **10**, 36–46.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. *JASA*, **58**, 236–244.

Wei, A. and Chow-Fraser, P. 2006. Synergistic impact of water level fluctuation and invasion of *Glyceria* on *Typha* in a freshwater marsh of Lake Ontario. *Aquat. Bot*., **84**, 63–69.

Willems, J. H., Peet, R. K., and Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci*., **4**, 203–212.

Eutrofeerumisest tingitud ajalistest ja ruumilistest muutustest Peipsi järve suurtaimede liigirikkuses

Helle Mäemets, Kadi Palmik ja Marina Haldna

Analüüsiti Peipsi järve taimestikus toimunud ajalisi ja ruumilisi muutusi, kasutades selleks 76 taksoni esinemissageduse (F) andmeid aastail 1970, 1980 ning 1997–2014 ja oletades, et liigirikkus on muutunud unimodaalselt, suurenedes järve eutrofeerumisel ning hiljem vähenedes. Selgus, et 35% liikidest kas ilmus või nende esinemissagedus suurenes kiire eutrofeerumise perioodil 1970. aastatel. Märgatavam tõus liikide arvus toimus järve lõunapoolsemates osades. Muutused Shannoni indeksis olid analoogsed liikide arvu suurenemisega ja (Pielou) ühtluse indeks ei näidanud eri uurimiskordade vahel statistiliselt olulist erinevust. Ajavahemikus 1970–2014 toimus 52 taimeliigil ja suurtel niitrohevetikatel Peipsi järves kas kogu vaatlusperioodi või selle lõike hõlmav statistiliselt oluline esinemissageduse muutus. Liikide arvu märgatav suurenemine järve lõunapoolsetes osades tulenes eelkõige kinnikasvavat litoraali asustanud tavaliste hügrofüütide, kaldaveetaimede ja amfiibsete liikide laiemast levikust. Tähelepanuväärne F-i suurenemine toimus liikidel *Phalaris arundinacea*, *Glyceria maxima*, *Sium latifolium*, *Agrostis stolonifera* ja *Rorippa amphibia* ning hüdrofüütidest peamiselt varjulisi kasvupaiku armastavatel liikidel *Spirodela*, *Hydrocharis*, *Lemna*, *Nuphar*, *Ceratophyllum*, *Sparganium*, *Stratiotes* ja *Elodea*. Kõikidel vaatluskordadel näitas samade 22 punkti võrdlus, et 1980. aastaks ilmusid suured niitrohevetikad, *Potamogeton gramineus*, *P. pectinatus* ja *Stratiotes*. Kui aastail 1970–1980 suurenes liigirikkus neis punktides märgatavalt, siis aastail 1997–2014 oli aasta keskmine liikide arv sarnane või väiksem kui 1980. aastal. Meie töö tulemused näitasid, et antropogeense eutrofeerumise algusaastail liigirikkus küll suurenes, kuid see tõus ei jäänud püsima.

Klasteranalüüsiga, mis baseerus 52 punkti ja 243 vaatluse andmetel aastaist 1997–2014 ning hõlmas 80 liiki, selgitati 40 indikaatorliiki, millega seostuvat kuut klastrit võib käsitleda tänapäeval Peipsile iseloomulike litoraali taimestiku tüüpidena/elupaikadena. Nende liigirikkus erines tunduvalt: liigivaestest roostikest (keskmiselt 7 liiki vaatluse kohta) avaranna ja rootukkade vaheldumisega liigirikaste kohtadeni (14–34 liiki). Järve kui terviku liikide arv pole küll vähenenud, kuid liigivaeste roostike pindala on suur. Liigirikkuse püsimist toetavad muutlik veetase ja mõõdukas inimmõju.