Eesti Maaülikool
Estonian University of Life Sciences

EFFECTS OF NATURAL AND ANTHROPOGENIC PRESSURES AND DISTURBANCES ON THE MACROPHYTES OF LAKE PEIPSI

LOODUSLIKE JA INIMTEKKELISTE SURVETEGURITE MÕJU PEIPSI JÄRVE SUURTAIMESTIKULE

KADI PALMIK

A Thesis
for applying for the degree of Doctor of Philosophy in Hydrobiology

Väitekiri
filosoofiadoktori kraadi taotlemiseks hüdrobioloogia erialal

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LIST OF ORIGINAL PUBLICATIONS

The present thesis is based on the following articles, which are referred to by their Roman numerals in the text. The articles are reproduced by the kind permission of the publishers.

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

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

III. Mämets, H., Palmik, K. & Haldna, M. 2016. Eutrophication-driven spatial and temporal changes in macrophyte diversity in Lake Peipsi. *Proceedings of the Estonian Academy of Sciences* 65: 394–407.

IV. Mäemets, H., Laugaste, R., Palmik, K. & Haldna, M. The response of primary producers to water level fluctuations and its reflection in ecological assessment. Submitted to *Proceedings of the Estonian Academy of Sciences.*

Author´s contribution to the articles:

Article	**I**	**II**	**III**	**IV**
Idea and study design		*	*	*
Data collection	*	*	*	*
Data analyses	*	*	*	*
Manuscript preparation	*	*	*	*

ABBREVIATIONS

F – species frequency
JSCs – Jaccard´s similarity
M – managed shore stretches
W – wild shore stretches
WL – water level
WLF – water level fluctuation

1. INTRODUCTION

The term 'aquatic macrophytes' refers to macroscopic forms of aquatic vegetation and encompasses macroalgae, a few species of mosses and ferns adapted to aquatic habitats, as well as true angiosperms (Wetzel, 2001). Aquatic plants have different life forms: emergent, submerged, floating-leaved, and freely floating, and their three major dispersal vectors are water, wind, and animals (Lacoul & Freedman, 2006). The littoral is the near shore zone of a water body and its depth limit mostly marks the distribution of macrophyte depth. Lake edges are considered as the most species-rich areas of water bodies (Vadeboncoeur et al., 2011). They include land/water transitory zones and contribute notably to total biodiversity (Schmieder, 2004a). Large lakes usually encompass a variety of microhabitats which create good conditions for different species and even though littoral habitats constitute a small fraction of total lake areas, the vast majority of fish and invertebrate species inhabit the shallow zone or are completely restricted to the littoral zone (Vadeboncoeur et al., 2011). These lakes, including Lake Peipsi (3555 km^2), play an important role in the dynamics of global biodiversity.

The importance of aquatic macrophytes cannot be overestimated because of their crucial role in promoting clear water, providing habitats for invertebrates, fish, and birds (Carpenter & Lodge, 1986; Jeppesen et al., 1998) and their contribution to the functioning and services of wetland ecosystems (Engelhardt & Ritchie, 2001). Macrophytes contribute to the functional diversity and habitat complexity, which plays an important role in determining diversity (Lucena-Moya & Duggan, 2011; McGoff & Irvine, 2009). The mosaic of habitat types creates a high degree of spatial heterogeneity (Brauns et al., 2007). For example, in relation to microfauna it has been suggested that higher abundance and taxon richness is characteristic of vegetated areas and increases with increasing complexity (Lucena-Moya & Duggan, 2011). Macroinvertebrate densities in plant beds have been described to be 4–5 times higher than in unvegetated sediments (Strayer & Malcolm, 2007). Moreover, littoral areas are important recruitment areas for fish; the findings by Randall et al. (1996) revealed significantly higher fish production, as well as greater species richness in the presence of high macrophyte abundance. Also, herbivorous birds are dependent on macrophyte species richness (Van Eerden & Bos, 2007). Additionally, aquatic plants affect nutrient cycling in the littoral (Horppila

& Nurminen, 2005; Human et al., 2015), and the littoral zone can supply the highest productivity in a lake (Wetzel, 2001). Besides submerged macrophytes also emergents have been found to be important in retaining water quality through reduction of sediment resuspension (Horppila et al., 2013; Horppila & Nurminen, 2001). Other factors favouring the focus on macrophytes in lake research include their importance in providing key services to freshwater ecosystems (Bornette & Puijalon, 2011) and the relevance of littoral areas for recreational purposes.

On the largest scale, all ecosystems undergo change and are subject to a number of natural or human-induced pressures. It is essential to assess the consequences of the human impact on species and the overall human-induced environmental change in freshwaters (Dodds et al., 2013). Taking into account that most human activities take place in the littoral zones, it is very important to integrate these zones into research, and by comparison with the open water zone (pelagial), the littoral regions of lakes have generally been less studied (Vadeboncoeur et al., 2011). Macrophytes can be effectively used as long-term indicators of the conditions to which they are subjected (Melzer, 1999) and are therefore important bioassessment components of the European Water Framework Directive. Their temporal and spatial distribution is affected by several environmental factors often defined as disturbances or pressures. The present thesis is an attempt to understand the reflection of these stressors in the change of species richness and abundance and the aim of the thesis is to cover a part of the natural and anthropogenic pressures and disturbances. It focuses on the effect of: a) water level (WL) changes; b) eutrophication, and c) reed removal. The naturally fluctuating water level has been considered to be a natural disturbance factor, and anthropogenic eutrophication and reed removal are the most important human-induced influences.

The availability of long-term sampling results reduces the impact of year-to-year variability (derived from natural factors) and the uncertainty of research findings (Søndergaard et al., 2016). The information about water level fluctuations (WLF) of Lake Peipsi dates back to 1885 (Jaani et al., 2008) and comparable data of macrophytes have been available since 1970. Thus, such a long-term data series of Peipsi enables researchers to evaluate the extent of environmental alterations, to understand the reflection of floristic changes in the lakes´ history, and to assist in determining the most probable driving factors. The principal importance of this study is its comparison of species richness before and after rapid eutrophication (**I, III**); explaining the response of macrophyte species richness and abundance to water level variation (**IV**), and ascertainment of the effect of reed management on macrophyte species richness (**II**).

2. REVIEW OF THE LITERATURE

2.1. Species diversity and its importance

The number of species found in a community or in an ecosystem is the simplest measure of diversity. However, the number is relatively less informative compared to species abundance. Species evenness, which expresses how evenly the individuals in the community are distributed over the different species (Heip et al., 1998), accounts also for species abundance and is an important diversity measure for assessing overall diversity.

In recent decades much attention has been paid to ecosystem services which in simple words could be explained as benefits of the ecosystem to people (Boyd & Banzhaf, 2006; Millennium Ecosystem Assessment, 2005). An important aspect when talking about biodiversity is how it helps to maintain the stability of ecosystem functioning and services. It has been demonstrated in grasslands that ecosystem functioning and sustainability is in peril due to species loss (Tilman et al., 1996). There is consensus that in changing environments a larger number of species becomes essential for the maintenance of stability (Loreau et al., 2001), and the insurance hypothesis summarizes the importance of biodiversity – acting as a buffer against environmental oscillations (Yachi & Loreau, 1999). McCann (2000) concluded that diversity does not increase the stability directly, but its impact depends on the ability of the community to provide the species or functional groups with the capability of differential response.

Macrophytes have an important role in water bodies and contribute to the functioning and services of wetland ecosystems (Engelhardt & Ritchie, 2001). Being a key component of aquatic ecosystems, macrophytes and their richness have a strong link to a number of ecosystem services, and it is important to determine the factors affecting macrophyte distribution.

2.2. Pressures and disturbances

All ecosystems undergo change and are subject to a number of natural or human-induced pressures and disturbances which are regarded as key processes leading to alterations. In many cases, in the ecological studies and in different contexts, disturbance has been used as a synonym for pressure or all the parameters which rule the occurrence of species are regarded as stressors. Schulte (2014) suggested that stressors should be regarded as environmental changes that cause reductions in the performance of organisms.

In general, pressure could be defined as a long-lasting influence and disturbance (perturbation) as a short-term or cyclic impact. According to a broad definition by Pickett and White (1985), disturbance disrupts an ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. Disturbances are also defined as unpredictable events, and Keddy (2010) claims that a disturbance is a short-lived event that removes biomass and thereby causes a measurable change in the properties of an ecological community. According to Keddy´s interpretation, eutrophication is not categorized as a disturbance, but could be regarded as a pressure. Both the changing WL and reed removal could be regarded as disturbances. In all cases duration, intensity, frequency, and area are considered to be important properties of disturbances (Keddy, 2010), and an intermediate disturbance has been found to maintain the highest level of diversity (Connell, 1978).

2.3. Influence of natural pressures and disturbances on the distribution of macrophytes

Below is an overview of several natural abiotic factors which may act as pressures or/and disturbances. The same factor may act as a pressure in one case and a disturbance in another. For example, light availability at high latitudes is seasonally limited and this pressure determines the prevalence of long-day plants. On the other hand, harmful algal blooms may cause extraordinary poor light conditions in some growing seasons as a disturbance. According to a study of inter-annual differences in *Potamogeton perfoliatus* L., the stands which were covered with thick mass of filamentous algae did not flower in the next summer (Mäemets et al., 2006). An important factor determining the zonation of aquatic plants is composition of bottom sediments (Spence, 1982), and species vary in their preference for sediment quality (Lacoul & Freedman, 2006). However, the type of bedrock, which determines the type of the littoral, and water depth, which modifies the impact of mechanical stress, both influence the formation of the bottom sediment. Thus, it is doubtful whether the sediment type could be regarded as a stressor. Factors which are important for the objectives of the current study are discussed in more detail than others .

Light has been considered to be one of the most important abiotic factors for macrophytes (Barko et al., 1982; Egertson et al., 2004), and light requirements of aquatic plants depend on their life form (Middelboe & Markager, 1997). Moreover, light conditions determine their distribution and colonization depth (Istvánovics et al., 2008). Also, the models developed for shallow lakes in the Netherlands revealed the importance of light extinction (Van den Berg et al., 2003). The presence of sufficient light is very important in spring because light stress due to phytoplankton development limits germination from the propagule bank (Robin et al., 2014). Despite the species-rich propagule bank, light stress by abundant phytoplankton causes lower species richness of macrophyte vegetation (Arthaud et al., 2012). The results by Van Nes et al. (2002) suggested that even a short clear-water phase raises the survival of vegetation, and it is more important in the period of maximal production than right after germination. In comparison, Lombardo (2005) revealed that midsummer Secchi depth was not related to macrophyte growth or phytoplankton biomass, indicating the importance of spring light conditions.

Besides light climate also **temperature** is of great importance for aquatic plants (Barko et al., 1982). It affects successfulness of reproduction (germination of seeds) and therefore determines the distribution and biomass of macrophyte communities. Light and temperature appear to interact in influencing macrophyte distribution and seasonal growth (Barko et al., 1982). A study on inter-annual variation of temperature (Rooney & Kalff, 2000) showed deeper macrophyte colonization and whole-lake biomass in relation to early season temperature increases. Moreover, temperature may have an indirect effect on macrophytes through affecting water chemistry (Pip, 1989). Climate change in relation to the contribution of growing degree-days can cause expansion of emergent aquatic macrophytes distribution (Alahuhta et al., 2011) and may have a profound effect on the other species. The rapid warming of lake surface waters in different regions and a concurrent increase in algal blooms (O’Reilly et al., 2015) may also contribute to the changes in submerged macrophytes.

Water level fluctuations reflect changes in the water regime of the catchment area and are dependent on weather conditions. Several studies have emphasized the importance of hydrological conditions on macrophytes (e.g. Coops & Velde, 1995; Riis & Hawes, 2002). Casanova and Brock (2000) tried to ascertain what affects most the development of plant communities and found that depth, duration, and frequency of inundation are all important, and the duration of an individual flooding event is substantial in segregating plant communities. Geest et al. (2005) detected higher species richness of submerged macrophytes in lakes experiencing drawdown.

Generally, wetland species have broad tolerance limits for the WL and they can establish themselves in different water depth gradients; however, some species have distinct germination requirements (Keddy & Ellis, 1985). The fluctuating WL in the eulittoral zone (the region between the highest and lowest seasonal water levels) has been described to affect the coverage and species composition of aquatic plants in reservoirs (Krolová et al., 2013), and shoreline vegetation can benefit from low-water periods through regeneration from buried seeds (Keddy & Reznicek, 1986). In Lake Kinneret, WL at germination and the rate of water fluctuation decided the dynamics of plant growth and the maximum biomass (Gafny & Gasith, 1999). Jutila (2001) revealed higher germination in the flooded treatment compared to the non-flooded one. He concluded that flood disturbance in combination with other abiotic factors may work as a dormancy breaking factor for some species. Exposed bottom and shallow water favour several small-sized rare amphibious and hygrophyte species, e.g. *Alisma gramineum* Lej., because seed reproduction after a water level decrease supports the success of seedling establishment (Moravcová et al., 2001). In general, temporary habitats are important for the viability of seed banks (Leck & Brock, 2000).

The WL decrease can cause significant changes in the proportions of functional groups of plants (Hudon, 2004). Partanen and Hellsten (2005) found a 49–73% increase in emergent vegetation in three lakes due to the spring flood reduction. A substantial increase in the area covered by emergents at the decreased WL was also detected by Egertson (2004). Emergent plants, such as the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), suffer from the submergence of young seedlings and any degree of submergence can be relevant (Armstrong et al., 1999). In addition, the common reed has been reported to germinate more successfully in low waters (Coops & Velde, 1995), and in the Great Lakes decreases in the WL and the bare soil area were associated with the expansion of *Phragmites* (Tulbure & Johnston, 2010). Remarkably, the pond-based experiment by Deegan et al. (2007) showed that reed prefers moderately fluctuating water levels because the largest biomass occurred in the ±30cm amplitude treatment. Thus, subsequent WLF create suitable conditions for growth and can promote the expansion of emergent vegetation (Coops et al., 2004). By contrast, unusual drought can cause delayed shoot emergence in spring, which results in lower density of reeds as well as incompleteness in matureness (Haslam, 2010).

An increased WL may affect plants through altered light availability in deeper water (Wersal & Madsen, 2011), and a high water level in spring may cause sparse vegetation (Coops et al., 2003). According to Brock et al. (1987), flooding caused the decline of a number of helophytes and summer inundations led almost to a complete disappearance of some aquatic macrophytes. Large reed declines were observed in Lake Constance due to extreme floods and high spring water levels in consecutive years (Schmieder et al., 2004b).

In large lakes one of the disturbance factors is **wave action**. In comparison with the pelagic area, the littoral is a shallower dynamic habitat where mechanical stress/disturbance by waves can have considerable influence. The impact of waves on plants depends on the actual WL (depth), wind fetch, and speed. Exposure to wind and waves was one of the most important environmental variables accounting for the total biomass of macrophytes (Hudon et al., 2000). According to Strand (1996), the decline in the biomass of *Potamogeton pectinatus* L. at high exposure was caused by physical wave action on the plants. Waves can cause direct physical damage and the uprooting effect, which affects the nearshore occurrence of submerged macrophytes (Chambers, 1987). Uprooting depends on the anchorage strength, which in turn is dependent on the cohesive strength of the sediment as well as the size of the root system (Schutten et al., 2005). As an adaptation, a decrease in shoot length and branching of *P. pectinatus* resulted from wave exposure (Idestam-Almquist & Kautsky, 1995). Redistribution of sediments by water movements may have a considerable effect on the composition of vegetation species because burial of propagules reduces the emergence of species and can in addition cause permanent loss of the propagule bank (Van Zuidam et al., 2014).

According to Keddy (1983), species richness peaks at intermediate levels of disturbance. In Axe Lake species richness of shoreline vegetation peaked at the intermediate level of exposure, having about twice as many species compared to more exposed shores (Keddy, 1983). Macrophyte development rates were consistently lower in the case of greater water depth and fetches (Rea et al., 1998). In parallel, the impact of exposure may be mediated. For example, Strand and Weisner (1996) found that the shoot biomass of submerged macrophytes was positively affected by exposure due to smaller production of epiphytic algae. At sheltered sites plants allocated more biomass to roots due to stronger competition from epiphytes (Strand & Weisner, 2001). At high exposure vegetation disappeared abruptly (Strand & Weisner, 1996).

Waves may also have other indirect influences on macrophyte development, causing sediment resuspension (Søndergaard et al., 1992; Tammeorg et al., 2013), which in turn can significantly reduce the emergence of species and the establishment of macrophytes in large lakes (Van Zuidam & Peeters, 2015). In the resuspension treatment by Van Zuidam and Peeters (2015) the emergence of *Chara* sp. and *Potamogeton pusillus* L. was reduced by 91% and 45%, respectively. On the other hand, the critical wind velocity required for sediment resuspension increases in the presence of vegetation (Barko & James, 1998). Resuspension rates in the stands of *P. pectinatus* by comparison with absence of macrophytes were very low even in the case of high wind speed (Barko & James, 1998), which affirms the importance of the presence of aquatic plants. The wave measurements in Lake Krankesjön also revealed that stands of *P. australis* can dampen wave height and wave breaking (Falås, 2007). Even relatively low densities of *Phragmites* may substantially affect water turbulence (Horppila et al., 2013).

Among natural disturbances also the effect of **ice** is relevant and species vary as to their sensitivity or tolerance towards winter drawdown (Mjelde et al., 2013). Mechanical damage by ice during low-water winters may lead to the disappearance of submerged macrophytes (Blindow, 1992a). Moreover, ice movements can cause modification of shoreline (Keddy, 2010). In addition to the direct effect of ice, the effect of ice phenology on macrophytes is notable, and, for example, mild winters may cause alterations in the vegetation structure, possibly causing expansion of shade tolerant and the decline of light-demanding plant species after several mild winters (Ejankowski & Lenard, 2016).

2.4. Influence of anthropogenic pressures on the distribution of macrophytes

The relationship between habitat trophy level, primary productivity, and species richness is described as a unimodal or hump-backed curve which generalizes that richness peaks at intermediate primary productivity and then decreases (Grime, 1973); thus, habitats with intermediate levels of biomass support the largest number of species. The same type of mechanism was proposed to be characteristic of lakes undergoing eutrophication (Sand-Jensen et al., 2008). Rajaniemi (2003) concluded that few plant species can tolerate very low resource levels and greater diversity occurs at intermediate productivity. Although partial recovery in species richness may be attained after positive changes (re-oligotrophication) in the environment, it is unlikely that the original species composition might recover (Sand-Jensen et al., 2017). Therefore, it is of crucial importance to pay attention to species composition not only to the species number. Unlike the trophic indices, diversity indices alone do not provide much information on the quality or impairment of the environment (Thiebaut et al., 2002).

Eutrophication is one of the main human-induced pressures deteriorating freshwater habitats worldwide (Smith, 1998, 2003) – the ecosystem´s response to the addition of plant nutrients by a significant increase in primary production (phytoplankton blooms, expansion of fast growing tall plants, etc.). Anthropogenic eutrophication has been a global problem for decades (Smith, 1998), and in Peipsi it started more intensively in the 1970s (Starast et al., 2001). Regarding macrophytes, some consequences of this process are analogous with the results of grassland fertilization.

Numerous grassland studies have described how nutrient enrichment causes an increase in vegetation density and reduces species richness (e.g. Foster & Gross, 1998; Stevens et al., 2004; Willems et al., 1993). Fertilization increases the abundance of tall runner species which eventually results in a decline in species diversity; however, there may be a lag in the species richness response (Dickson & Gross, 2013). Also, Zobel (1992) argued that the presence of taller species affects species richness via competition. Moreover, also the amount of litter is an important determinant of species richness and may hinder seed germination (Neuenkamp et al., 2013). A similar pattern is characteristic of water bodies where competitive and highly productive dominants occupy large areas. Species have specific sensitivity or tolerance to eutrophication (Penning et al., 2008a). Excessive nutrients can cause the dominance of a strong competitor *P. australis*, forming mono-specific stands, which in turn induces a decrease in species richness. It is one of the most widespread perennial plant species in the world (Haslam, 2010), highly competitive and capable of rapid growth and spread. It can tolerate highly different growth conditions and is common in both fresh and brackish waters (Haslam, 2010). The expansion of reeds during the past decades has been documented in many studies (Andersson, 2001; Chambers et al., 1999; Feldmann & Mäemets, 2004; Liira et al., 2010; Mäemets & Freiberg, 2004; Rice et al., 2000). Also, Alahuhta (2011) confirmed the expansion of emergents through colonization of new areas and predicted that this process would likely continue in the 2050s as a result of climate change. In the large shallow Peipsi, the increase in reeds has been the most remarkable consequence of nutrient enrichment during the past fifty years (Mäemets & Freiberg, 2004). Similarly to grasslands, accumulation of the (reed) litter may be an important factor in determining the species composition of littoral zones (Lenssen et al., 1999).

The expansion of reed has increased the need for the implementation of **reed management** in residential shoreline. In Peipsi the management scheme includes reed removal, burning the material, pushing the sand and other mineral sediments up the shore and forming a 'terraced' area. These activities are regarded as human induced influence.

According to the 'centrifugal model' (Keddy, 2010; Moore et al., 1989), tall and productive plant species dominate in the core habitat, and many small-sized plants live arrayed around the core habitat in peripheral areas. Due to high competition in core habitats, rare and declining species are characteristic of the peripheral areas where the biomass is low and biological diversity is supported by different disturbances (Keddy, 2010). Keddy pointed out that peripheral habitats are at risk due to anthropogenic eutrophication and increasing plant biomass. Any disturbances which can create gaps in the dominant species would let other, previously suppressed, species colonize new favourable sites (Keddy, 1983).

Excess nutrients in terrestrial and aquatic ecosystems cause diversity loss through competition for light (Hautier et al., 2009). Lake Müggelsee witnessed a gradual decline in species diversity from ca 24 to 5 species (Hilt et al., 2013). Jeppesen et al. (2000) found that the richness of submerged macrophytes declined monotonically with an increase in total phosphorus in water and phytoplankton blooms. In Lake Lugano, lost species belonged to submerged plants as well as to emergents (Lachavanne et al., 1992). In Denmark, the total occurrence of charophytes decreased by 56% in the course of eutrophication (Baastrup-Spohr et al., 2013) and from the shallow Lake Veluwemeer charophytes disappeared completely during the period when the phosphorus concentration increased (Van den Berg et al., 1999). However, smaller species of charophytes (*Chara contraria* A. Braun ex Kütz., *C. aspera* Dethard. ex Willd. etc) can persist also in eutrophic lakes with a high phosphorus content but are restricted to shallow water (Blindow, 1992b). Charophytes may reappear after the reduction of nutrients (Sand-Jensen et al., 2017).

Also the appearance and proliferation of filamentous green algae indicate anthropogenic eutrophication (Dodds & Gudder, 1992; Jupp & Spence, 1977), and, for example, outbreaks of *Cladophora* may play a significant role in structuring the plant community (Hansel-Welch et al., 2003). Also, Sand-Jensen et al. (2017) noted the dominance of macroalgae such as *Cladophora glomerata* (Linnaeus) Kützing and *Enteromorpha flexuosa* (Wulfen) J.Agardh during eutrophication. In Lake Windermere the biomass of *Cladophora* revealed seasonal variation in relation to phosphate availability (Parker & Maberly, 2000). However, the possible influence of some other environmental factors such as availability of light, temperature, WL can not be excluded.

Excess of nutrients, such as an abrupt increase in nitrogen does not cause toxicity, but macrophyte loss is probably caused by increased shading by filamentous algae, periphyton, and phytoplankton (Olsen et al. 2015; Yu et al. 2015). Besides changes in abundance and diversity, the dominance structure of species is affected by nutrient over-enrichment (Niemeier & Hubert, 1986). In the Clear Lake, agricultural eutrophication caused a community composition shift from submergent to floating-leaved, and with increasing eutrophication to emergent-dominated flora (Egertson et al., 2004). In Lake Võrtsjärv, during the eutrophication process the earlier broad-leaved dominant *P. perfoliatus* among the submerged plants was replaced by *Myriophyllum spicatum* L., which has finely divided leaves (Feldmann & Mäemets, 2004; Feldmann & Nõges, 2007). Strong eutrophication can favour the proliferation of unrooted macrophytes and induce change in the lake type (Mäemets & Freiberg, 2005). In addition, also Rintanen (1996), based on his long-term study in Finland, revealed changes in botanical lake types in the course of eutrophication (from oligotrophic types towards eutrophic ones). In Lake Fure Sand-Jensen (2008) found a decrease in the species number of hydrophytes and dominance of tall angiosperms following nutrient enrichment. Also, Wallsten (1981) demonstrated substantial differences in macrophyte vegetation in Swedish lakes during 40 years, mainly expressed by an increase in emergent vegetation and a decrease in elodeids. However, Sand-Jensen et al. (2017) found that the tall elodeid species was the only group which maintained unaltered richness during eutrophication. Besides species loss in the course of eutrophication, some species also appear as newcomers, e.g. *P. pusillus*, *P. pectinatus*, *Zannichellia palustris* L. (Rintanen, 1996).

3. AIMS OF THE STUDY

Lake Peipsi has undergone anthropogenic eutrophication which has largely contributed to the changes in the lake´s biota, including macrophytes. Moreover, naturally fluctuating water level and reed removal are the factors that add to the possible changes in species richness of macrophytes. The present study focused primarily on the changes in the richness of macrophyte species in the lake under natural (fluctuating water level) and anthropogenic (eutrophication, reed eradication) disturbances and pressures.

This study aimed to:

1) Provide an analytical overview of changes in the macrophyte species composition of Peipsi in the course of eutrophication (**I**) and to reveal the changes during its rapid process (**III**).
The author hypothesized that the species number increases at the beginning of eutrophication and decreases or stabilizes during the later periods.

2) Assess the human impact on macrophytes in relation to reed removal by comparing species richness and composition in managed and wild shore areas (**II**).
The author hypothesized that management supports the maintenance of declining species.

3) Assess what kinds of changes in macrovegetation are correlated with water level and to which extent can extreme water level fluctuations affect their biomass (**IV**).
The author hypothesized that the low water level results in a significant increase in the occurrence and abundance of macrophytes.

4. MATERIALS AND METHODS

4.1. Description of the study area

Lake Peipsi (surface area 3555 km^2, mean depth 7.1 m, maximum depth 15.3 m) is located on the border between Estonia and Russia (Fig.1). Peipsi is the fourth largest lake in Europe and consists of three parts which differ in morphometry, hydrology, trophic state, and composition of biota (Kangur & Möls, 2008). The largest and deepest northern part, Lake Peipsi *sensu stricto* (Peipsi *s.s.*) is eutrophic, the southernmost part Lake Pihkva hypertrophic, and the river-like Lake Lämmijärv reveals intermediate characteristics (Jaani et al., 2008). The average volume of the whole Peipsi is 25 km^3 and the water residence time is about two years. The WL is unregulated, the amplitude of fluctuation in annual average of the water level during the period 1890–2005 was 1.5 m, and the overall range is about 3 m (Jaani et al., 2008). For this reason 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 metres is available for inhabitation by shore plants at the lowest WL. In Peipsi, similarly to 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 period is usually considerably lower than in spring (Jaani et al., 2008). The data from 1939/1940–2005/2006 show that the ice cover lasts in average 118 days (Jaani et al., 2008), from the end of November until the second half of April. The height of waves at the prevailing summer wind speed (5 m s^{-1}) is 40–60 cm in Peipsi s.s. and 20–30 cm in Lämmijärv, and due to long fetches (e.g. the length of Peipsi s.s is 80 km and the average width is 32 km) their impact may be remarkable (Jaani et al., 2008).

The bedrock of the lake basin consists mostly of Devonian sandstone, but in the northernmost and southernmost parts also outcrops of Ordovician and Devonian limestone are present. The lake bottom is mainly formed of silty and sandy sediments and in some smaller areas also of clay or peat (Raukas, 1999).

The trophy level of Peipsi has increased step by step from the mesotrophic-eutrophic state to the eutrophic-hypertrophic state during the past decades, depending on the lake part (Kangur et al., 2002; Kangur & Möls, 2008;

Leeben et al., 2012; Milius & Haldna, 2008; Tammeorg et al., 2013). The northern part, Peipsi *s.s.* was mesotrophic until the 1970s (Mäemets et al., 1996) and eutrophic during the previous decades. The southernmost part, Pihkva was earlier eutrophic (Kangur et al., 2007) but hypertrophic in the past decades and Lämmijärv displays intermediate characteristics. Changes in the content of orthophosphate ions, nitrate and nitrit ions revealed that the rapid anthropogenic eutrophication of Peipsi began in the early 1970s (Starast et al., 1999).

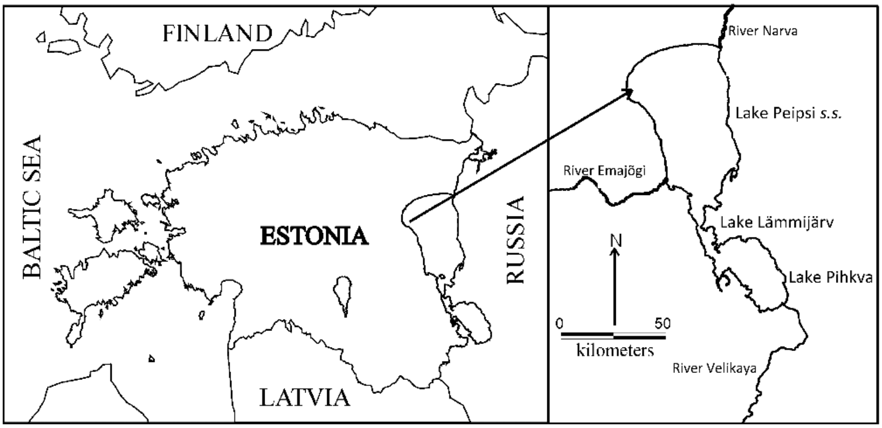

Figure 1. Location of Lake Peipsi (adapted from Kangur & Möls, 2008).

4.2. Data and macrophyte sampling

4.2.1. Macrophyte data for long-term comparisons

In order to detect changes in the composition of macrophyte species over a longer period of time, the historical material based on the studies by Aime Mäemets in 1970, 1971, and 1980 was used. Altogether 50 stations over the whole lake were studied repeatedly in 1970 and 1980, and 37 additional stations in different stretches were studied in the years 1970, 1971, and 1980. On the basis of this data, the frequency (F) of 67 taxa over 87 stations was calculated for the whole lake, which was used for the comparison with F (139 stations) in 1997–2007 (**I**). Additionally, the newest monitoring data (up to 2016) was used to reveal contemporary species frequency. Furthermore, the floristic data collected by Tuvikene

(1966) in 1962–1963 and Nedospasova (1974) in 1966–1970 were used for revealing changes in the species composition. The author of the present thesis has participated in all of the field studies since 2005.

Article **III** analysed the differences in the F of species between three periods: 1970, 1980, and 1997–2014 to detect changes in the course of the beginning of eutrophication and later. For this purpose we compared F of macrophyte taxa in 49 stations studied by Mäemets (1970 and 1980) and in 52 stations studied by the authors of the article (1997–2014). These stations represented all three parts of the lake (Peipsi *s.s.*, Lämmijärv, and Pihkva) and most of them were visited repeatedly in 1997–2014. Among all the old and new stations the location was the same for 22 stations (Fig. 1 in **III**). In general, all the studies surveyed macrophytes annually in July or at the beginning of August. Samples of orthophosphate ion were analysed at the Institute of Zoology and Botany in 1965–1992 and at the Tartu Department of the Estonian Environmental Research Centre in 1992–2014.

In all the studies herbaceous species were registered starting on the shore, from the edge of bushes and trees, until the last occurrence (as seen from a boat) of the stands of submerged plants (mainly *P. perfoliatus*). Submerged plants were sampled by using a plant hook (as shown in Katanskaya, 1981) with a graded rope. The relative abundance of taxa per station was estimated on a five-point semi-quantitative scale of Braun-Blanquet and the criteria were as follows: 1 – single plant or 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. One has to emphasize the term 'relative' as the scale used was not identical to the coverage scales Braun-Blanquet or DAFOR but displays the importance of a species in the corresponding group (emergent, submergents, etc.). The abundance of macroscopic filamentous green algae was estimated for every station according to the same scale (0–5) but separately from submerged macrophytes due to the different life/growth form. Additionally, the width of the reed belt was measured with a tapeline and the number of reed shoots was counted in two 1x1 m quadrats.

4.2.2. Macrophyte data for the comparison of wild and managed shore areas

The study concerning the effect of reed removal on macrophyte species richness was conducted in the north-western part of Peipsi in Vilusi village (Fig. 1 in **II**). The area has a flat till shore and its macrophyte species richness is considerably high. According to local people, *P. australis* was first noticed on the shores in the 1970s and started to spread vigorously, presently forming reed beds about 100 m wide. This has increased the necessity from holidaymakers and local people to manage the lake shores more actively. In the studied area the first reed removal took place in 1993 and the most recent one in 2008.

The information about the management was collected from the local residents. The main scheme included uprooting of reed (and other plants) by using a bulldozer, burning the material, and pushing the sand and other mineral sediments up the shore and forming a 'terraced' area between the dunes and the water edge. Such a 'terrace' and its slope are important determinants of the success of reed removal. After about every 2–4 weeks the area was mowed between the months of May and September.

Floristic composition and species richness of managed and wild shore areas were compared. The study area was located between the border of dry sand dunes and a shallow littoral zone. In 2006 and 2008, all shore taxa in the different properties were registered as a total number, and in 2009–2010 more detailed transect investigations were carried out, with quadrats of 0.5 m×0.5 m with intervals of 9.5 m. The number of randomly chosen transects varied from 11 in 2009 to 12 in 2010, and the study included nine M and three W stretches. Most of the M areas consisted of the following zones: (a) mowed 'terrace'; (b) intermediate area, and (c) water. The total number of the studied quadrats was 124 in 2009 and 135 in 2010. The number of quadrats per transect varied from 10–15, that is, the width of a study area was 100–150 m from the dune edge up to a water depth of 0.6 m in 2009 and 0.8 m in 2010. Coverage (%) estimations of all taxa were recorded and the abundance of large filamentous algae was estimated using the Braun-Blanquet scale. In addition, water depth was registered. The frequencies of taxa were calculated. In managed stretches 22 observations were made, compared with 7 of wild stretches. The taxa which were found to differ between W and M stretches less than twice in F were excluded and also those with low find numbers as 0–1, 0–2, and 1–2. A more detailed description of the method can be found in article **II**.

Depending on different sensitivity to the human impact, the species were divided into four ecological groups as follows: (a) hemerophobes – species that avoid urban environment; (b) hemeradiaphors – species that are neutral to the human impact; (c) anthropophytes – species introduced by humans, and (d) apophytes that are synanthropic plants favoured by disturbed habitats (Kukk, 1999). Considering the need of water supply for plants, the following division was used: (a) xerophilous – tolerating dry habitats; (b) mesophilous – the water supply is neither scanty nor abundant; (c) hygrophilous – living in a wet or very moist ground, and (d) hydrophilous – living in water (Usher, 1996).

4.2.3. Data for studying the effect of water level fluctuations on macrophytes

Article **IV** assessed the effect of WLF on macrophyte species richness and abundance, including the years of 2005–2015 from ten stations (Fig. 1 in **IV**). The relative abundance was estimated according the methods described in 4.2.1. Additionally, for the detection of differences in biomasses at low and high WL values from published datasets (Mäemets & Freiberg, 2004; Mäemets et al., 2006) and reports of the Estonian State Monitoring Programme were used (**IV**). For the calculation of biomass of submerged plants and large filamentous algae, data collected by SCUBA diver in 1999–2002 were used. All above-ground parts of the submerged plants were collected from quadrats of 0.5 x 0.5 m in two replicates (Mäemets et al., 2006) and maximum (in 1999) and minimum (in 2000) WLs of this period were close to the maximum and minimum of the study period in 2005–2015. For the calculations of the biomass of pondweeds and macroalgae a hypothetical "compressed" belt width of 20 m between the reed belt and the open lake was used, assuming that this zone of 10 km^2 is under water all the time and that in the most favourable years it is covered by submerged stands more or less continuously.

Given the particularity of Lake Peipsi, the quality classes according to the national macrophyte method are based on the occurrence and abundance of different macrophyte species and abundance of filamentous green algae (order document N° 44 by the Estonian Minister of the Environment). The indicative value of species was considered similarly to the

Central-Baltic intercalibration summary (G.-Tóth et al., 2008). For Peipsi the abundant occurrence of small-sized amphibious plants (*A. gramineum, Ranunculus reptans* L.) and hygrophytes (*Juncus* spp., *Eleocharis* spp.), as well as *P. perfoliatus*, *P. gramineus* L., and *P. filiformis* Pers. is considered to indicate a 'good' status. On the other hand, abundant filamentous algae, microscopic epiphytic algae, monospecific reeds, *Typha* spp., floating plants, and ceratophyllids indicate a 'poor' status.

4.3. Data analyses

For analysing long-term changes in species frequencies the Wilcoxon Signed-Rank test was used to determine the distribution of frequency. For comparison of the proportion of each species the Z-value was applied (**I**).

In article III, in order to assess differences in species diversity between the different lake parts and the study times, the number of species, Shannon diversity, and Pielou's evenness were estimated and tested by using ANOVA. To estimate the temporal effect of sampling site, year, phosphates and water transparency on the macrophyte species composition, non-parametric multivariate analysis of variance using permutation tests for distance matrix (Bray-Curtis dissimilarity measures on the basis of species abundances) was used (adonis function in R package vegan). Species frequency and the significance of its change were tested for the whole lake and also separately for the three parts of the lake (Peipsi s.s., Lämmijärv, and Pihkva). Cluster analysis with Euclidean distance and Ward´s method (1963) based on the abundance of macrophyte species was used to clarify the source of variability. The resulting clusters were characterized as contemporary habitat types.

In the study of macrophytes at Vilusi (**II**) the difference in the ecological division of the taxa between the M and W shore stretches was tested using the chi-square test (Plackett, 1983). Proportional analysis (Z-test) was used for comparison of species frequency for each taxon between the M and W areas. An analysis of floristic similarity among all the M and W stretches (2006, 2008) and transects (2009–2010) was carried out using Jaccard's similarity coefficients (JSC). 31 stretches/transects were compared by their pairs and then clustered by Ward's method (1963) on the basis of $JSC = C/(A + B-C)$, where A and B denote the species number in samples and C is the number of species shared by the two samples. The criterion for statistical significance was set at the 5% level.

The changes in macrophyte abundance related to WLF (**IV**) were tested by Spearman's correlation analysis. All observations (n=110) and also the sum of the relative abundance of species per year (n=11) were used to test the correlations (at the significance level 0.01). The generalized linear model (SAS/STAT GENMOD) with repeated measures for the sampling sites was used to estimate the specific effect of WL on macrophyte abundance, considering the effect of sample sites random. The Poisson distribution was used for macrophyte abundancies and the dispersion parameter was estimated by Pearson's chi-square statistic divided by its degrees of freedom.

5. RESULTS

5.1. Eutrophication effects on macrophytes in Lake Peipsi

The analysis of the macrophyte data (articles **I** and **III**) indicated that considerable changes in species composition are probably caused by the continuing expansion of thick reeds in Peipsi. Also, the data collected in the course of the national monitoring in 2005–2015 revealed ongoing densification (linear regression, $p < 0.0001$) of *P. australis* stands (Fig. 2). Occupation of the littoral by thick reeds has caused a decrease in suitable eulittoral habitats for several characteristic species of Peipsi (e.g. *Ranunculus reptans*, *P. gramineus, Eleocharis palustris* (L.) Roem. & Schult., *Polygonum amphibium* L.) (Article **I**).

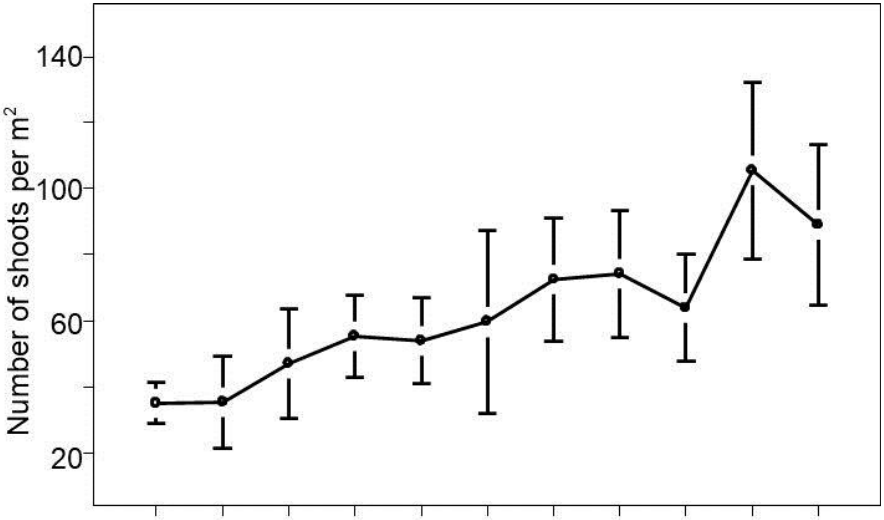

Figure 2. Average number of reed (*Phragmites australis*) shoots per square metre with 95% confidence limits of ten monitoring stations of Lake Peipsi (locations shown in Fig. 1 in Article **IV**) during the period of 2005–2015.

Comparison of the periods 1962–1980 and 1997–2007 revealed disappearance of the two most sensitive hydrophyte species *Isoëtes echinospora* Durieu and *Subularia aquatica* L. (Article **I**), which were still present in the lake in the 1960s. A further study, including data until 2014, reconfirmed their disappearance (Article **III**). On the other hand, eutraphent *Lemna gibba* L. appeared during the past decades.

The impact of eutrophication on the vegetation was expressed mainly in the change of F of many species. The rank of species according to their F changed profoundly. Comparison of the frequency data from all 87 studied stations from the periods 1970–1980 (first published in 1999 by Mäemets & Mäemets) and 1997–2007 (139 stations), revealed a significant decline of F for 20 taxa (**I**). According the data used in article **I**, the group of the most frequent species (F 47–100%) included 17 taxa in 1970–1980 and only three in 1997–2007. More than half of the significantly declined taxa dropped at least 10 places lower on the frequency list in 1997–2007 (**I**). According to the latest F calculations, using additional data of the past 10 years, that is, 1997–2016, the frequency group 47–100% included 10 taxa. Figures 3a and 3b present 46 species, selecting the most frequent taxa and some species with remarkably changed F. Apart from the significantly declined taxa, for example *Ceratophyllum demersum* L., *Spirodela polyrhiza* (L.) Schleid. and *Hydrocharis morsus-ranae* L. revealed a significant increase in frequency, indicating the effect of eutrophication.

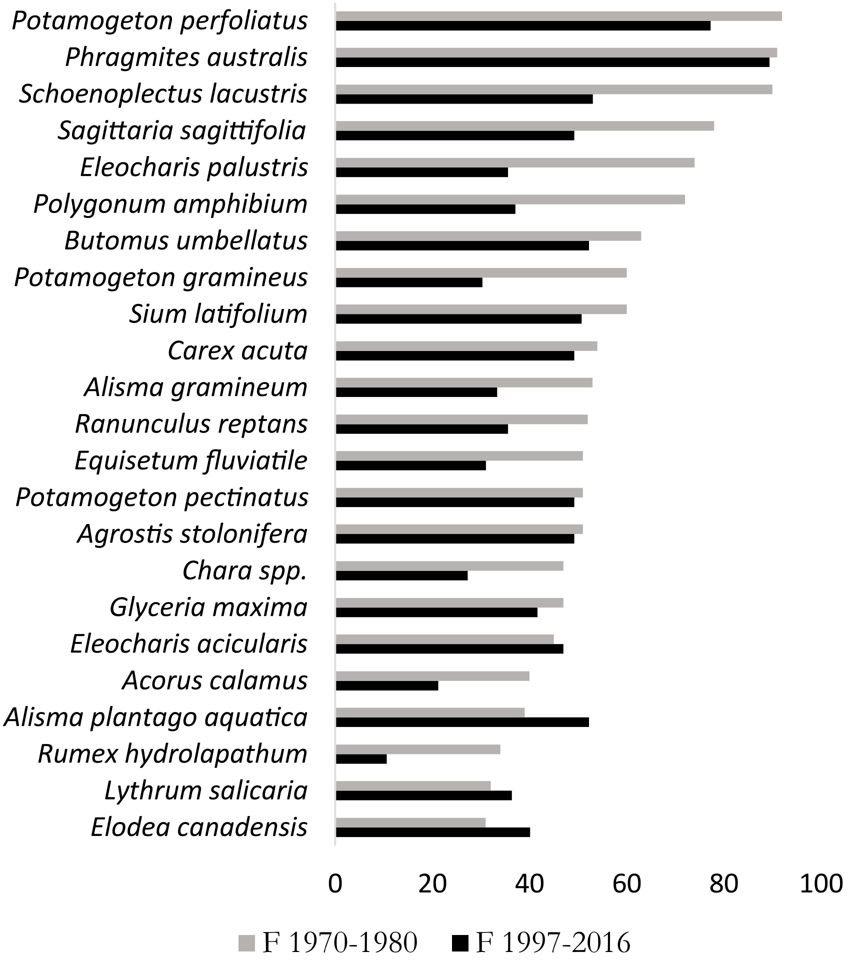

Figure 3a. Frequency of taxa in Lake Peipsi in 1970–1980 and 1997–2016.

After analysing F changes in more detail, more taxa (67→76) was added and a similar number of stations in three study times: 49 in 1970 and 1980 versus 52 in 1997–2014 was selected. The data of three periods revealed appearance or a significant change in the frequency of 53 vascular taxa after 1970 (**III**). The most rapid change took place between 1970 and 1980 and the main increase occurred in the F of common hygrophytes, helophytes, and amphibious plants. In parallel, an increase in the F of filamentous green algae was observed. Since 1970 the proportion of helophytes in the taxa lists has increased and the share of amphibious

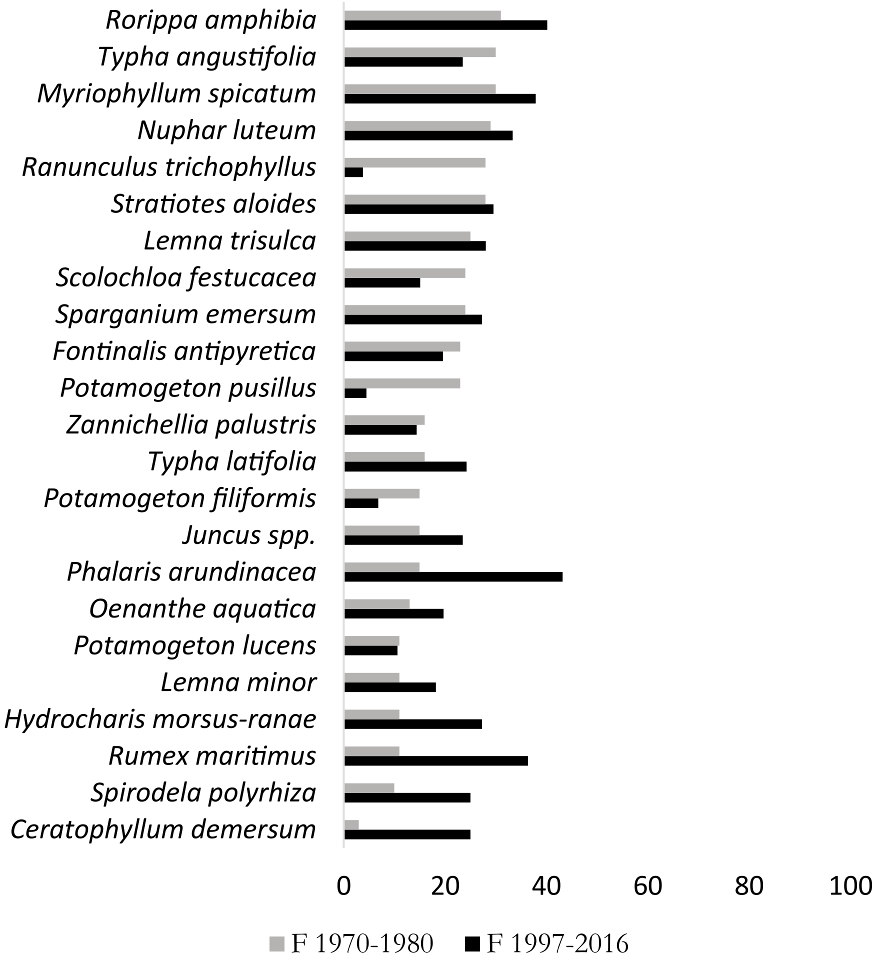

Figure 3b. Frequency of taxa in Lake Peipsi in 1970–1980 and 1997–2016.

plants has decreased (**III**). The comparison of different lake parts showed a clear increase in the species number in Pihkva and Lämmijärv; however, in Peipsi *s.s.*, which was already the richest in species, the increase was not that notable (Fig. 4a). Changes in Shannon´s diversity were analogous to the dynamics of the species number, and species evenness showed only a slight insignificant decline in the southern parts of the lake (Fig. 4b, c). The results of statistical analysis indicated a significant ($p = 0.001$) effect of the sampling site, year, phosphates, and water transparency on species composition in different time periods (Article **III**).

In the 22 stations around the lake which were the same in all the study times, the biggest change took place also between 1970 and 1980, revealing at least a twofold increase in the species number in 14 stations (Table 1). Besides numerous hygrophytes and helophytes also several hydrophytes such as *P. pectinatus*, *P. gramineus*, *Stratiotes aloides* L. as well as filamentous algae occurred in 1980. In some stations the species number revealed a decrease after 1980; however, there were also stations with a minimal change (Table 1). Repeated observations (1997–2014) yielded larger numbers of species per station, but the average species number per year was similar (Lake Pihkva) or lower (Peipsi s.s. and Lämmijärv) in comparison with 1980, and the total average for 22 stations showed a decreasing trend.

The clustering of observations in 1997–2014 revealed that the eutrophication of Peipsi has created species-rich habitats (type 1: average species No 21, range 6–57) in sheltered places among the stands of helophytes where several floating and floating-leaved plants are common (Table 5 in **III**). Similar vegetation was found in Vilusi where floating plants such as *Lemna minor* L. and *Spirodela polyrrhiza* grew mainly in shaded wild areas (**II**). In parallel, wide thick reeds have created extremely species-poor habitats (type 3: average 7, range 3–16). The most species-rich (average 34, range 26–41) was habitat type 6, which included different sub-ecotones: open sandy littoral in one side and reeds in the other side of Värska bay, and the non-managed mesotrophic floodplain (Table 5 in **III**). Habitat types 2 and 5 represent intermittent reed stands and open shore stretches, and the characteristic species include *P. gramineus*, *C. contraria*, and large filamentous algae. Remarkably, the division of observations (according to species composition) between clusters 2 and 5 depended on the year and thereby on the water level (**III** and **IV**).

Table 1. Number of macrophyte species in Lake Peipsi in the same 22 stations at different study times. *including species of sedge meadow; **cleaned boat canals.

Stations	1970	1980	Average No of species per year 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	

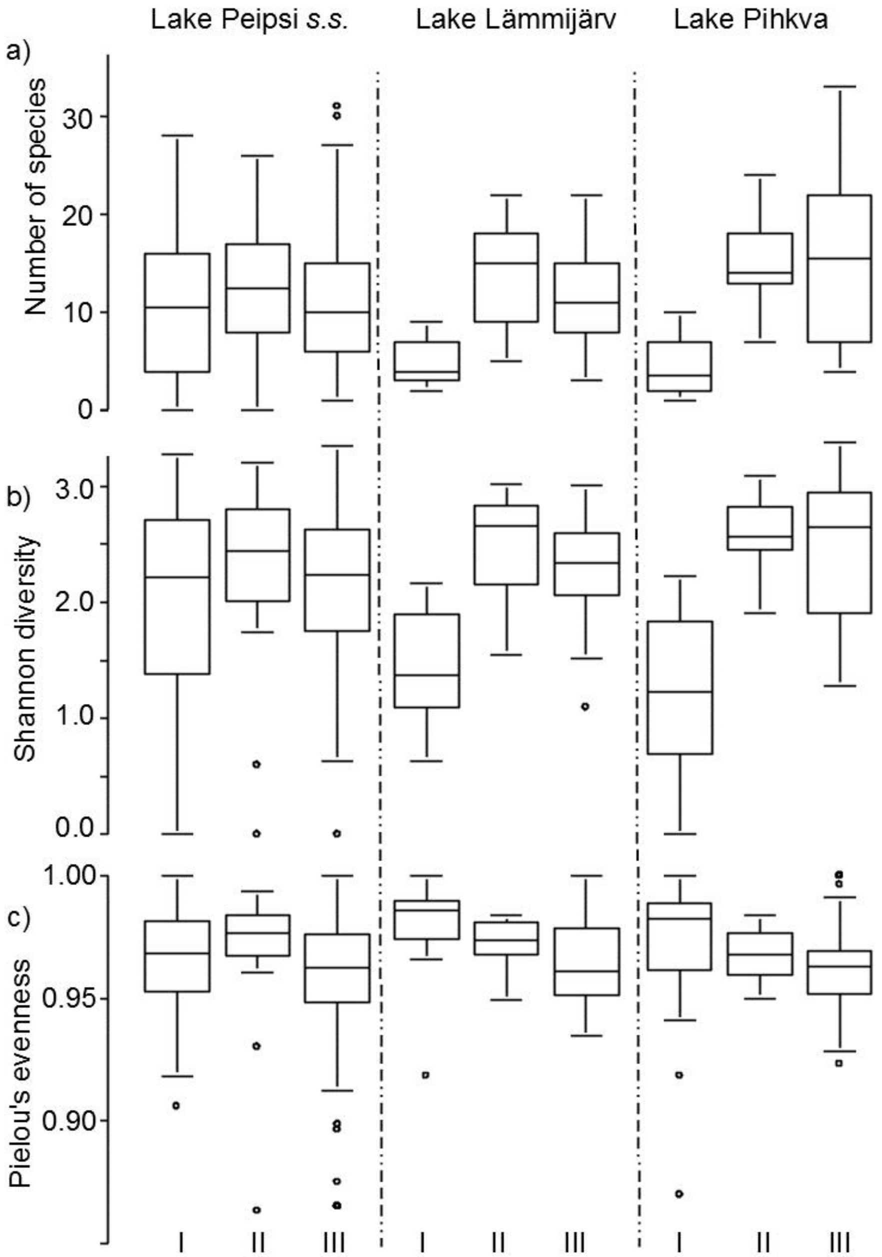

Figure 4. Average number of macrophyte species per station in different lake parts at different study times (a), Shannon diversity index (b) and Pielou´s evenness (c). Box plots indicate median values and interquartile ranges while whiskers show 5% and 95% quantiles. The Roman numbers: I – 1970; II – 1980; III – 1997–2014.

5.2. Effect of reed management on species richness

During the study period, in total 107 species were found in M and W shore stretches. Considering the difference in species composition, 37 taxa were found only on M, 8 only on W stretches, and 59 taxa were present in both types. Jaccard´s similarity coefficient (JSC) between M and W was 0.57.

Along the (all M and W) transects, the average number of taxa was the highest in the mowed intermediate zone (the average number per quadrat = 11) and in the mowed 'terrace' (= 9). Comparison of different management styles revealed the highest species richness in the stretches without 'terrace' or with a variety of M and W habitats (Fig. 5 EL, SL, SLw).

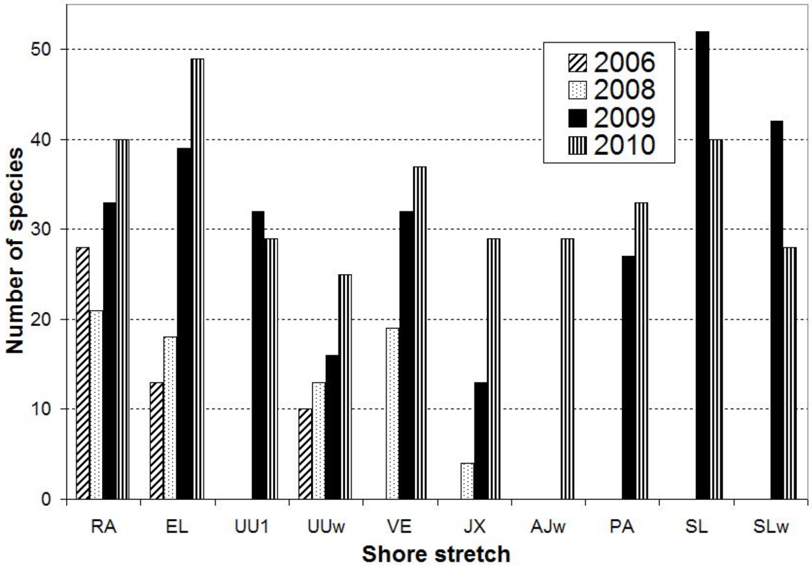

Figure 5. Total number of macrophyte taxa for different shore stretches (abbreviations represent the names of the owners; the letter 'w' indicates a wild stretch).

More diverse species groups (Fig. 4 in **II**) were represented in the M areas than in the W areas. All xerophytes were present only in the M areas, as well as a larger proportion of the mesophytes. The proportion of apophytes was slightly higher in the M than in the W stretches. Among the apophytes *Glyceria maxima* (Hartm.) Holmb., *Lemna minor*, *L. trisulca* L., and *Spirodela polyrhiza* were more characteristic of the W areas (Table 2). These species inhabit sheltered fertile W places and are also common in boat canals, river mouths, and helophyte mazes and are characteristic species of habitat type 1 (**III**). Thus, these species grow in the areas which are formed due to the succession: nutrient enrichment → increase of reeds and other fast-growing macrophytes → formation of sheltered habitats.

Among hemeradiaphors, many small-sized species such as *Eleocharis uniglumis* (Link) Schult., *Ranunculus reptans*, *Juncus spp.*, *Cyperus fuscus* L. (Table 2.) occurred mainly in the M stretches. Tall helophytes were characteristic of W, submerged and amphibious plants were common in the M areas. Management supported the occurrence of some other declining species such as *Eleocharis palustris*, *A. gramineum*, and *C. contraria*.

Table 2. Frequency (%) of apophyte and hemeradiaphor taxa in wild (F_W) and managed (F_M) shore stretches. Growth forms: A – amphibious; FL – floating; H – helophytes and hygrophytes; S – submerged. Plant size: M – medium; S – small; T – tall. * – protected species.

Taxa	F_W	F_M	Growth forms	Plant size
Apophytes				
Alisma plantago-aquatica	0	45	H	M
Agrostis stolonifera	14	82	H	S
Carex hirta	0	41	H	M
Eleocharis palustris	0	50	H	M
Glyceria maxima	100	27	H	T
Lysimachia vulgaris	71	32	H	T
Mentha arvensis	29	73	H	M
Myosotis scorpioides	14	73	H	M
Sagina nodosa	0	36	H	S
Sagittaria sagittifolia	14	32	A	M
Sonchus spp.	0	34	H	M
Stachys palustris	71	32	H	M
Sium latifolium	0	32	H	T
Phalaris arundinacea	57	32	H	T
Lemna minor	71	5	FL	
Lemna trisulca	57	9	FL	
Potamogeton pectinatus	29	68	S	
Spirodela polyrrhiza	57	5	FL	

Taxa	**F_W**	**F_M**	**Growth forms**	**Plant size**
Hemeradiaphors				
*Alisma gramineum**	14	41	A	M
Calamagrostis canescens	43	0	H	T
Carex acuta	71	32	H	T
*Cyperus fuscus**	14	32	H	S
Eleocharis uniglumis	0	59	H	S
Juncus articulatus	0	36	H	S
Juncus spp.	14	82	H	S
Lycopus europaeus	0	50	H	M
Lysimachia thyrsiflora	57	0	H	M
Lythrum salicaria	57	18	H	T
Ranunculus reptans	0	32	A	S
Rumex hydrolapathum	57	0	H	T
Rumex maritimus	0	32	H	M
Salix seedlings	0	41	H	S
Scolochloa festucacea	43	14	H	T
Chara contraria	14	50	S	S
Hydrocharis morsus-ranae	57	0	FL	
Myriophyllum spicatum	0	45	S	
Potamogeton perfoliatus	14	82	S	

The findings based on Jaccard's similarity coefficients revealed inter-annual differences for the shore and littoral vegetation and the JSC values varied between 0.30–0.50 for the whole study area **(II)**. Floristic similarity among all ownerships and transects for the whole study period was dependent on the year (water level) along with a similar style of management (Fig. 8 in **II**).

5.3. Effects of water level fluctuations

The WL changes of Lake Peipsi have a seasonal pattern (Fig. 6), and the study period of the present thesis (2005–2015) included notable WL differences between years.

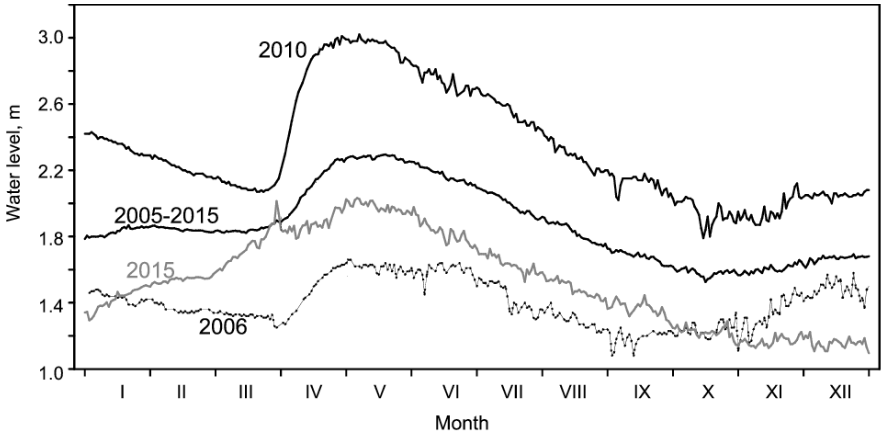

Figure 6. Seasonal dynamics of the water level of Lake Peipsi in some extreme years and its averaged course in 2005–2015.

The naturally fluctuating WL in Peipsi can cause remarkable changes in the eulittoral, and during the study period of the thesis (2006–2010) the shore area became up to 30 m narrower due to WL increase (Article **II**). Studies **II** and **III** indicated that the yearly changing WL caused differences in species dominance and determined the plant zonation in the littoral.

The analysis of the data collected in 2005–2015 (**IV**) revealed that species richness of submerged macrophytes and the total number of species was significantly related to WLF ($p < 0.01$). The results of modelling predicted a 1.6…4-time increase in the abundance of several species at a 1 m decrease in WL (Table 3). The maximum, fourfold increase occurred for *Chara contraria*.

Table 3. The 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 (May–August).

Variables	**Results of GENMOD**	**n = 110**
	Estimated ratio with conf. 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
Potamogeton perfoliatus	1.6 (1.1–2.1)	0.03
Potamogeton pectinatus	2.5 (1.5–4)	0.026
Myriophyllum spicatum	3.4 (1.7–6)	0.01
Chara contraria	4 (1.6–10)	0.038
Large filamentous algae	3.1 (1.7–5)	0.014

The abundance of several macrophyte species and large filamentous algae increased at low WLs (Fig. 7a, b). Remarkably, nutrient-demanding *Zannichellia palustris* and *P. pectinatus* occurred more frequently at a low water level. In addition, a strong relationship between the appearance of *L. gibba* (indicative of eutrophic conditions) and a low WL was noticed.

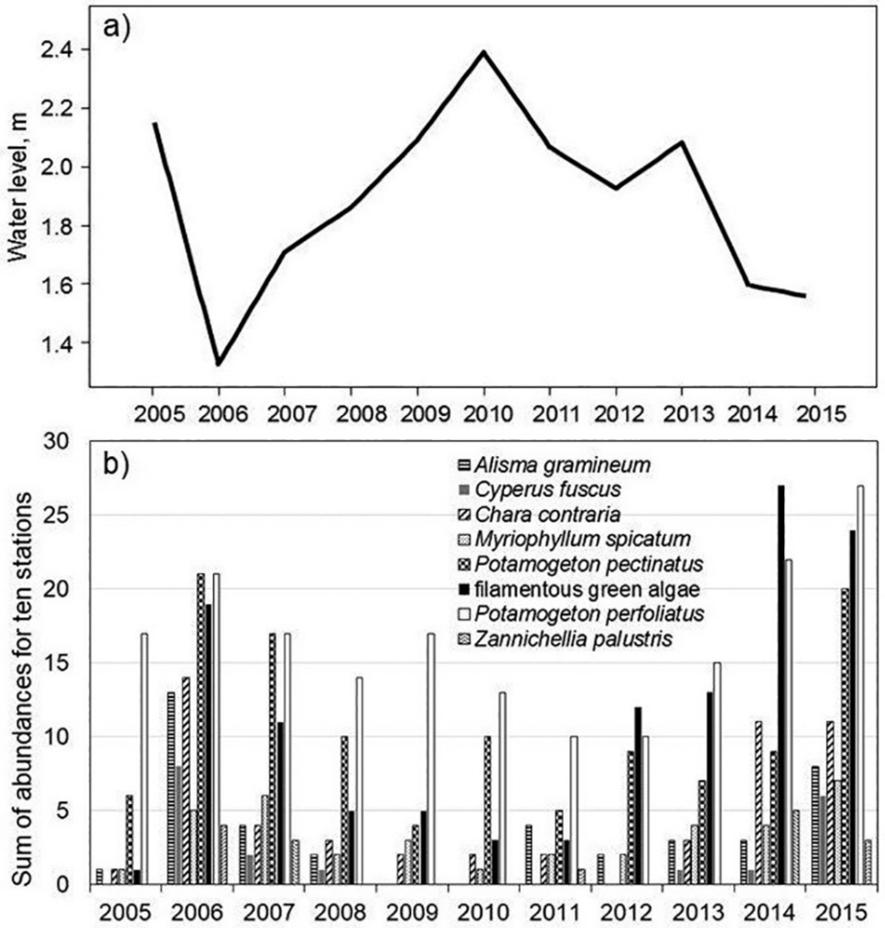

Figure 7. Summertime (July–August) water level of Lake Peipsi (a) and occurrence of taxa (b) that showed a significantly different abundance between the years (summarized abundance estimates by a modified scale of Braun-Blanquet for every year, all 10 stations together).

In addition to changes in species richness with a WL decrease, biomass comparisons of *Potamogeton* at extreme WLs revealed a 2.2 times higher biomass with the lowest WL. Similarly, large filamentous algae showed a big shift from almost no occurrence at the high WL to considerable abundance and biomass at a decreased WL (**IV**).

The aforementioned notable differences in the abundance influenced greatly the assessment of the ecological status of Peipsi. Based on the abundance of large filamentous algae it varied from ‘poor’ to ‘high’ in 2006 and 2010, respectively, revealing the importance of WL change (**IV**).

On the other hand, at low WLs the abundance of submerged macrophytes and occurrence of declining species indicated the ‘good’ status, but the nutrient-demanding *L. gibba* was characteristic of the ‘poor’ status.

Besides the aforenamed changes, also the width of the *Phragmites* belt on the northern coast displayed clear yearly oscillations (Fig. 6. in **IV**), but it was not significantly correlated with the WL. In the southern part of the lake, where a large part of reed grows in deeper >1 m water, tangled and yellowing reed was observed with the rising WL.

6. DISCUSSION

6.1. Eutrophication-linked changes in macrovegetation

The results of the present study indicate that eutrophication caused considerable changes in the aquatic vegetation of Lake Peipsi, and among pressures and disturbances affecting macrophytes it had profound long-lasting consequences. The importance of eutrophication on macrovegetation has been shown in several other lakes (Hautier et al., 2009; Lachavanne et al., 1992; Sand-Jensen et al., 2008, 2017).

Contrary to central European lakes where severe reed decline has been documented (Kubín & Melzer, 1997; Ostendorp et al., 1995), the reeds in Peipsi have considerably increased due to anthropogenic eutrophication. The increase in the proportion of helophytes in Peipsi during eutrophication had direct influence on other macrophyte species. The findings of the present thesis led to similar conclusion as the study by Kolada (2016) who found that helophytes represent an added value in the evaluation of the ecological status of lakes under eutrophication pressure. The proliferation of reed has diminished suitable littoral habitats for small-sized species of which *Isoëtes echinospora* and *Subularia aquatica* disappeared. In addition to species that became extinct, some new species (e.g. *Lemna gibba*) appeared, reflecting nutrient enrichment of the lake. Similarly, in Finnish lakes with nutrient enrichment some eutraphent species such as *Zannichellia palustris* and *P. pectinatus* were found as newcomers (Rintanen, 1996). In Peipsi, these species occur more abundantly at a low WL.

A slight inconsistency between the results of **I** and **III** regarding the number of species with a significant decrease in F may derive from different reasons. 1. The second study (**III**) was based on a smaller but comparable number of former and recently studied stations to distinguish composition changes between the investigations in 1970 and 1980 and the latest period. 2. In study **I** joint frequencies of 1970 and 1980 were used – the latter representing the time after the occurrence of numerous species.

Despite this inconsistency, floristic impoverishment due to the proliferation of thick reeds is expressed by the presence of contemporary habitat type 3, the poorest in species, in the case of wide and thick reeds (habitat type 3 in **III**). Most of the typical representatives of the macrophyte flora of Peipsi grew in the stations where the shore is partially reed-free.

The author of the thesis tested the hypothesis that species richness increases at the beginning of eutrophication and decreases or stabilizes in the later periods. Anthropogenic eutrophication really increased the average species number of macrophytes in the beginning, but the later decrease (hump-backed species richness curve – Grime, 1973) was more clearly expressed in the comparison of 22 stations (**III**). The total species richness in Peipsi did not decrease due to the formation of new habitats and the appearance of several medium-sized or large fast-growing plants and lemnids by 1980, which became common in the flora of Peipsi. Other supporting factors include removal of reed by landowners, cleaning of boat canals, and the cyclic naturally fluctuating WL (receding WL), which creates suitable conditions for several species (**II** and **IV)**.

Similarly to other studies (Nozaki et al., 2003; Parker & Maberly, 2000; Planas et al., 1996; Sand-Jensen et al., 2017), nutrient enrichment in Peipsi accounted for the abrupt increase in the abundance of filamentous green algae. Also, in Windermere the biomass of *Cladophora* revealed seasonal variation in relation to phosphate availability (Parker & Maberly, 2000).

In general, the idea of negative influences of filamentous algae on aquatic plants is widely accepted. By contrast, Hansel-Welch et al. (2003) found that *Potamogeton* spp. and the species of *Chara* had a positive association with annual variation in the abundance of filamentous algae. They argued about the positive effect of competition between filamentous algae and phytoplankton on stoneworts, possibly due to the enhanced light climate. The findings of the present thesis (**IV**), however, suggest that the occurrence of all groups: *Potamogeton*, *Chara,* and filamentous algae is supported by low water due to the increase in mineral nutrients (resuspension, enhanced bacterial decomposition), light availability, and better germination of propagules at the low WL, and that the positive impact of filamentous algae on the *Chara* and *Potamogeton* is doubtful. Moreover, the results of the present thesis reveal that phytoplankton blooms and abundant occurrence of submerged macrophytes may be simultaneous (**IV**). It has been widely described how nutrient over-enrichment changes the succession pattern of aquatic plants, and richness of submerged macrophytes decreases dramatically (Jeppesen et al., 2000), and community composition shifts appear due to eutrophication (Egertson et al., 2004). The findings of the thesis suggest that theory of alternative stable states

(Scheffer et al., 1993) does not work in large shallow lakes such as Peipsi with a naturally fluctuating WL. Janssen et al. (2014) concluded that lakes with prevailing size effects generally lack macrophytes, and alternative stable states are unlikely to occur there but WLF can drive alternating behaviour of lakes to eutrophication.

6.2. The effect of reed removal on macrophyte species richness

Given that *P. australis* is a large leafy species with a high competitive ability, the result of the present thesis concerning the positive effect of reed removal on medium- and small-sized species in Peipsi was somewhat expected. The same pattern revealed itself in the experiment by Farnsworth and Meyerson (1999) where species composition of the removal plots was richer compared to the intact areas. Also, in Estonian coastal grasslands (overgrown by reeds) managed and restored sites revealed higher species diversity (Sammul et al., 2012). The positive effect of management was revealed on such species as *Agrostis stolonifera* L. and *Juncus gerardii* Loisel. (Enno, 2016). Similarly, in the present study *Agrostis stolonifera* and *Juncus* spp. were much more abundant in M stretches.

Although in general *Phragmites* as a strong competitor with a higher success rate limits the growth of neighbouring species, in the fen experiment by Güsewell and Edwards (1999) light interception (shading) by reed did not reveal any strong effect on the existence of other species until June. They concluded that coexistence with the common reed could still enable high diversity if other species express faster development in spring and achieve matureness before *Phragmites* canopy develops. The results of the present thesis indicate that it depends on the height and density of the reed, which has also increased in the past decades in Peipsi, and in such areas the assumption of high diversity communities coexisting with thick *Phragmites* stands is not probable. In Peipsi, vegetation of sheltered habitats (**III**) emerges between the lakeside reed and shore vegetation. In addition to shading, dense stands of *Phragmites* alter the habitats by increased build-up of litter and by the change of soil properties in combination with the WL (Lenssen et al., 1999).

The 'centrifugal model' of Keddy (2010), according to which tall and productive plants (species) dominate in a core habitat and many small-sized plants live arrayed around the core habitat in peripheral areas, is also characteristic of Peipsi. Similarly to other studies (e. g. Moore et al., 1989), anthropogenic eutrophication in Peipsi has put species of peripheral areas at risk, and disturbances such as WLF provide new opportunities to suppressed species. At large natural WLF appearing in Peipsi these peripheral areas emerge periodically, supporting the species richness.

Species have different sensitivity to human impact and in general apophytes are synanthropic plants favoured by disturbed habitats. However, regarding the results of this thesis, several apophytes were more characteristic of wild areas compared to the managed ones. Given that the lakeshore of Peipsi is a naturally disturbed habitat due to WLF, the number of apophytes does not clearly couple with management regimes. This sheds light on the possibility that in water bodies the apophytic character of some species is related to possible indirect human impact, for example, eutrophication, which supports the presence of some apophytic plants in fertile wild habitats between reeds.

Minchinton and Bertness (2003) found that in order to control the expansion of reed stands, the focus should be set on reducing nutrient loads, but in the areas where dense reed beds already exist and show rapid spread, the removal of plants would be the only reasonable control method. The same applies for Peipsi where monodominant reeds have expanded in the course of anthropogenic eutrophication. Also, it is of crucial importance to harvest and remove plants from the shores in order to prevent nutrient release during decomposition and to avoid oxygen deficit during rapid decomposition (Pokorný & Květ, 2004).

The second hypothesis of this study was confirmed as M shore stretches supported the presence of small amphibious plants and hygrophytes. However, the removal of all larger stands would reduce the nesting areas of several bird species. Moreover, the intake of nutrients and the release of N_2 by denitrification are important attributes of reeds (Findlay et al., 2003).

Comparing the different techniques of reed removal, one might conclude that the formation of dry ‘terraced’ areas, even if favoured by locals, should not be the first choice due to its negative effect on species richness at the low WL. Although many macrophyte species have viable soil seed banks (Kaplan et al., 2014), such management techniques (terrace building) may still pose a risk for the further survival of species (burial of propagules) and inhibit regeneration. Moreover, too frequent mowing may perturb the seed production of annual species.

The use of a lakeshore for recreation through swimming, fishing, tourism, etc. is very important for people, and near Peipsi we can expect even an increased interest in the coming future in retaining the recreational value of these areas through removal of nuisance reeds. Therefore, the results of the present study concerning the impact of different management styles have great practical importance. Current results allow to recommend that the implementation of management practices should also focus on keeping the heterogeneity of the littoral habitat for combining the success of shore cleaning and maintenance of species richness. Understanding the ecological impact of reed removal is a prerequisite for the sustainable management of lakeshores simultaneously for recreation and nature protection. Littoral areas of the lakes also offer different regulating (e.g. water purification) and supporting (e.g. primary production, habitats for species) services (Kiviat, 2013) where macrophytes have a substantial role to play. The study of the impact of the WLF revealed that the intensity of these services varies remarkably year after year.

6.3. Impact of water level fluctuations

The findings of the present thesis suggested that although reed removal is an important factor for the persistence of species-rich communities, it is likely that also WLF might play a substantial role. Thus, natural factors may have an important influence on the effect of management.

The author of the thesis found that WL-related changes in Peipsi are in accordance with the intermediate disturbance theory (Connell, 1978), supporting the highest level of diversity (**IV**). Also Zhang et al. (2015) detected the effect of WLF as an intermediate disturbance that creates a more heterogenic environment and decreases interspecific competition. Flood-pulse adaptation of lake littoral species allows sequential use of this zone by different species (Wantzen et al., 2008), which fosters biodiversity. Changes in WL create new ecological niches and a mosaic of habitats, leading to a high community richness (Keddy & Reznicek, 1986; Trémolières, 2004). Especially annual plants are subject to considerable variations in abundance over time and are favoured by WLF. Exposure of lakeshore is favourable for species which rely on reproduction by seeds, and they become successful in temporary habitats. Also, it was characteristic of protected species such as *Alisma gramineum* and *Cyperus* *fuscus* (**IV**), which probably would not be able to persist without exposed littoral zones in between otherwise monotonous reeds. These temporary habitats (after water has receded) on overgrowing shores are crucial for their development unless supported by shore management (**II**). Similarly to the results of the present thesis, Hroudová et al. (2004) found that the best conditions for seed production for *A. gramineum* are shallow water and recently exposed shores.

Different plant species have different requirements for the water level and sediments. For example, in Lake Kinneret it was described as a 'window of opportunity' for species to develop their maximum biomasses if the previously listed requirements were met (Gafny & Gasith, 1999). In addition to increased species richness, the abundance and biomass of several macrophyte species increased significantly at the low WL also in Peipsi, which confirmed the hypothesis that the low water period results in a significant increase in the ocurrence and biomass of macrophytes (**IV**). Thus, in Peipsi the 'window of opportunity' is a WL change that affects many species positively. Similarly, Havens et al. (2004) found a significant biomass increase of submergent macrophytes after drawdown. Also, in Peipsi *Chara contraria* responded quickly and became abundant, in addition to the increase of the biomass of other submerged species (**IV**).

According to Raven and Taylor (2003), the bloom-forming macroalgae (including *Cladophora*) belong to ruderals and they have the ability to profit from high resource availability in transient environments. The abundance of filamentous green algae in Peipsi increased considerably when the WL receded and the ratios of biomasses at the lowest and the highest WL were 2.2 for *Potamogeton* spp. and 2.6 for phytoplankton (**IV**). One can presume that enhanced decomposition and mineralization of organic matter in the case of the decreased WL supports primary producers. This result highlights once more the effect of WLF as a disturbance factor. One can suppose also the importance of WLF for the sedimentation of organic matter (e.g. reed litter) in sheltered areas. Macrophyte beds and algal mats provide a suitable refuge and feeding conditions for invertebrates (Pieczyńska et al., 1998); thus, big inter-annual differences in their abundance manifested by WLF can substantially shape the relationships of littoral organisms.

Appreciable increase in macrophytes was observed at a 1 m decrease in the water level, however, for example, in the Yuqiao Reservoir in China already a 0.5 m decline in the WL increased the maximum biomass of *Potamogeton crispus* L. by 21.3% (Zhang et al., 2015). Similarly, Van Geest et al. (2005) revealed significantly higher richness of submerged macrophytes in lakes with partial drawdown than in lakes with no drawdown, but floating-leaved plants and helophytes were not positively affected. Although the author of the thesis did not find a significant correlation between reed width and WLF, remarkable oscillations of reed width between the years of different WL were observed. Studies on reed dynamics have emphasized the importance of WLF, but it has been attributed mainly to the enhanced colonization by seedlings (Alvarez et al., 2005; Armstrong et al., 1999). The WL of the main growth phase of reed (Schmieder et al., 2004b) may be important too.

6.4. Macrophytes as environmental indicators in Lake Peipsi – some practical conclusions

Although several macrophyte species have strict habitat preferences, there are also examples where the same species may be present in eutrophic as well as in oligotrophic water bodies, therefore reducing their indicative value. Different national indices may cause differences in assigning quality classes for the same sites (G.-Tóth et al., 2008). On the European scale Penning et al. (2008a) assessed species sensitivity or tolerance to eutrophication, and even though the existence of reliable indicators was confirmed, some inconsistency still appeared, possibly affecting the assessment of ecological status (Penning et al., 2008b). Similarly to other countries (e. g. Kutyła, 2014 and references therein), the assessment of the ecological status of Peipsi is calibrated against eutrophication indices. However, in the light of the results of the present study of the year-to-year oscillations of macrophyte abundance (**IV**), the estimations of ecological quality may be in synchrony with natural disturbances. In Peipsi the appearance of indicator species is strongly affected by WLF; thus, the estimations of the ecological status between different years is more influenced by WLF than by the change in its trophic state. In Peipsi the indicator of deteriorated water bodies, large filamentous algae proliferate at the low WL, and at the same time the richness of submerged plants (indicators of a good status) increases together with the occurrence of some protected species (*Alisma gramineum* and *Cyperus fuscus*). We cannot argue the overall indicative value of macrophytes, but one has to highlight the effect of WLF as a potential factor governing the differences in ecological assessment based on aquatic plants in Peipsi – the low water years compared to the high water years may result in different conclusions. Therefore, annual studies of the vegetation instead of an interval of several years provide an opportunity to avoid erroneous conclusions.

In general, for the detection of eutrophication impact species abundance has been regarded as a much more sensitive indicator compared to species richness (Kolada et al., 2011). However, based on the results of the present study concerning the year-to-year differences in macrophyte abundance, it remains challenging to assess ecological quality under the influence of the naturally changing WL. For example, Søndergaard et al. (2010; 2016) acknowledged the response of many macrophyte metrics to eutrophication; however, the uncertainty of indicators has to be considered due to possibly large year-to-year variations. If the impact of WLF of Peipsi is not been considered in the status assessment, it may cause a somewhat biased interpretation of estimations; thus, the need for improved methodology might be justified.

CONCLUSIONS

The present thesis discusses the changes in macrophyte species richness and biomass in Lake Peipsi governed by different natural and anthropogenic pressures and disturbances.

Based on the results the following conclusions can be drawn:

1) The anthropogenic eutrophication of Peipsi has had a profound effect on macrophytes. It has induced the expansion of reeds, which in turn decreased suitable eulittoral habitats for other species (**I**, **II**, **III**).

2) During the rapid eutrophication between 1970 and 1980, the frequency of common hygrophytes, helophytes, and amphibious plants increased, as well as the frequency of filamentous green algae. The increase in the proportion of helophytes caused the formation of new sheltered habitats for nutrient-demanding hydrophytes (**I**, **II**, **III**).

3) Anthropogenic eutrophication increased the species number of macrophytes in Peipsi in the beginning, but the hump-backed species richness curve (later decrease in species richness at ongoing increase of trophy level) was clearly expressed only in some stations. Therefore, the first hypothesis of this work was found to be only partly true, as the results depended not only on the eutrophication but also on the location in the lake. Species richness in Peipsi persists due to the removal of reed, cleaning of boat canals, and the naturally fluctuating water level (**III**).

4) Comparison of the total number of species on wild and managed transects revealed higher species richness in managed stretches. Reed removal supported small threatened amphibious plants and hygrophytes which confirms the earlier hypothesis. Among the different management styles the highest species richness was revealed in the stretches without ‘terrace’ or with a combination of managed and wild habitats.

5) The importance of the water level in Peipsi for species richness is comparable with the management type. Floristic similarity was dependent on the management style as well as on the year (water level).

6) Changes in the water level create new ecological niches and a mosaic of habitats. Water level fluctuation as an intermediate disturbance factor supports species richness of macrophytes in Peipsi (**IV**). At low water habitats emerge for otherwise declining species (e.g. *Alisma gramineum*, *Ranunculus reptans*, *Cyperus fuscus*, etc.).

7) The abundance of the main submerged macrophytes, charophytes and large filamentous algae increased considerably at the low water level, as well as the species richness, supporting the third hypothesis.

8) The present study demonstrated that the periodically changing occurrence of macrophyte species and increasing/decreasing biomass derives from water level fluctuation. Therefore, the occurrence of indicator species and its influence on the estimation of ecological quality are in synchrony with the natural disturbance factor.

The results of the present thesis provide a basis for the recommendations for shore management. Probably interest in creating and retaining recreational areas near Peipsi will increase in the coming years. One might recommend that the implementation of shore management should focus on keeping littoral habitat heterogeneity for combining the success of shore cleaning and maintenance of species richness.

Considering the results of the present thesis about year-to-year differences in the occurrence and abundance of primary producers derived from water level fluctutation, their importance in ecological assessments should be considered more carefully, and the need of improved methodology is justified.

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SUMMARY IN ESTONIAN

LOODUSLIKE JA INIMTEKKELISTE SURVETEGURITE MÕJU PEIPSI JÄRVE SUURTAIMESTIKULE

Paljud ökosüsteemid on muutumises ja ohus inimtegevuse tagajärjel, mis võib mitmeid protsesse ka otseselt mõjutada ja kiirendada. Veekogude inimtekkeline rikastumine taimetoiteainetega on üks suurimaid mõjureid kogu elustikule ja veeökosüsteemide toimimisele. Samal ajal võivad ka looduslikud tegurid (nt veetaseme ja temperatuuri muutused ning jääolud) muutustes olulist rolli mängida. Võrreldes maismaa- ja veeökosüsteeme, peetakse viimaseid isegi enam ohustatuteks.

Suurjärvedes on mitmekesised biotoobid, mis pakuvad ka inimestele olulisi ressursse ja teenuseid. Veekogu kaldavöönd on liigirikas üleminekuala ehk ökotoon, mida peale taimede asustavad enamik suurselgrootute liike ja paljud kalaliigid. Litoraalialasid peetakse mitmekesiseima elustikuga ja kõrgeima bioproduktsiooniga vööndiks.

Makrofüüdid ehk suurtaimed on palja silmaga nähtavad veetaimed, millel on väga oluline roll nii vee keemiliste omaduste mõjutajana kui ka elu- ja varjepaigana ning toidubaasina paljudele teistele liikidele. Seepärast on oluline jälgida suurtaimestikus toimuvaid muutusi ning tuvastada looduslike ja inimtekkeliste survetegurite osa nende kujunemisel.

Töö põhineb Peipsi järve pikaajalistel uuringutel. Antropogeensete surveteguritena on töös käsitletud eutrofeerumist ja pilliroo eemaldamist ning loodusliku häiringuna veetaseme kõikumist.

Töö eesmärgid olid:

1) anda ülevaade eutrofeerumise mõjul Peipsi suurtaimestikus toimunud muutustest (**I**) ning välja tuua suundumused kiire eutrofeerumise perioodil (**III**);
2) hinnata roo eemaldamise ja terrassistamise (kalda kõrgemaks lükkamise) mõju taimestiku liigirikkusele (**II**);
3) selgitada veetaseme kõikumisest tulenevaid muutusi makrofüütide liigirikkuses ning biomassis (**IV**).

Analüüsiks kasutati Aime Mäemetsa varasemaid suurtaimestiku andmeid aastatest 1970–1980 ning uuemaid monitooringuandmeid perioodist 1997–2014. Pilliroo eemaldamise mõju taimestiku liigirikkusele uuriti võrreldes majandatud ja majandamata alasid Peipsi loodekäärus Vilusi külas.

Töö tulemused võib kokku võtta järgnevalt:

1) Peipsi järve antropogeenne eutrofeerumine põhjustas taimestikus suuri muutusi, millest üks olulisemaid oli rooalade laienemine. See omakorda vähendas eulitoraalis väikesekasvulistele liikidele sobivaid elupaiku.
2) Kiire eutrofeerumise perioodil (1970–1980) suurenes oluliselt tavaliste hügrofüütide, helofüütide, amfiibsete liikide ning suurte niitrohevetikate esinemissagedus. Helofüütide osatähtsuse tõus ning tekkinud uued varjulised elupaigad olid eutrofeerumise ilminguks.
3) Inimtekkeline eutrofeerumine Peipsis küll suurendas makrofüütide liigirikkust selle algusaastail, kuid järgnev liigirikkuse vähenemine troofsuse edasisel tõusul, mida on täheldatud maismaa taimestiku uuringutes, ilmnes vaid osades uurimispunktides. Liigirikkuse püsimist toetavad uute elupaikade teke, roo eemaldamine, paadikanalite puhastamine ja looduslikult muutlik veetase.
4) Majandatud ja majandamata rannaalade võrdlus kajastas suuremat taimestiku liigirikkust majandatud aladel. Kõige liigirikkamad olid rannalõigud, kus niidetud ja majandamata elupaigad vaheldusid ning ei olnud terrassistatud ala. Veetaseme kõikumise mõju Peipsi taimestiku liigirikkusele on võrreldav majandamise mõjuga. Floristiline sarnasus uuritud rannalõikude vahel oli sõltuvuses nii majandamistüübist kui ka aastast (veetaseme mõju).
5) Veetaseme kõikumised Peipsis on käsitletavad keskmise häiringuna, mis toetab liigirikkuse säilimist elupaikade suurenenud mosaiiksuse ning liikidele uute niššide kujunemise tõttu. Madalveeperioodil paljanduvad elupaigad, mis on sobivad muidu väheneva levikuga liikidele (näiteks *Alisma gramineum*, *Ranunculus reptans*, *Cyperus fuscus*).
6) Liigirikkus ning mitmete makrofüütide ja suurte niitrohevetikate ohtrus tõusid madalveeperioodil märgatavalt.
7) Meie uuring näitas suurtaimestiku liikide esinemise ning biomassi väga tugevat sõltuvust veetaseme muutustest. Seega on indikaatorliikide esinemine ning sellel põhinev veekogu ökoloogilise seisundi hinnang märkimisväärselt mõjutatud sellest looduslikust häiringufaktorist.

Arvestades, et viimastel aastakümnetel on Peipsi rannaaladel roo eemaldamine hoogustunud, tuleks varasemast suuremat tähelepanu pöörata selleks kasutatavatele meetoditele, kombineerimaks parimad lahendused ranna puhastamiseks ning liigirikkuse säilimiseks. See võimaldaks hoida elupaikade heterogeensust.

Uuringust ilmnes veetaseme kõikumise oluline mõju taimestiku liigirikkusele ning ohtruse muutustele järves. Peipsi ökoloogilise seisundi hindamisel suurtaimestiku järgi on olulisel kohal niitrohevetikate rohkus ning taimeliikide esinemissagedus, mis meie mitmeaastase uuringu põhjal on selgelt sõltuvuses veetaseme kõikumisest. Teades ökoloogilise seisundi hinnangu olulist sõltuvust veetasemest, tuleks hindamiskriteeriumeid täiustada.

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Eutrophication and macrophyte species richness in the large shallow North-European Lake Peipsi

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ABSTRACT

We present an overview of long-term changes in the floristic composition and growth areas in L. Peipsi (3555 km^2, unregulated water level) that have occurred since the 1960s and a list of plant taxa containing 140 species of higher plants and 4 charophytes. A significant correlation was found between the relative abundance and frequency per stations (Fs) (Rs = 0.93). Data on five inhabitants of the eulittoral revealed significant ($p < 0.05$) inter-annual differences in Fs. Comparison of the data of Fs for 67 taxa for 1970–1980 (87 stations) and 1997–2007 (139 stations) showed a significant change in the Fs distribution ($p < 0.03$) and a decline ($p < 0.05$) for 20 taxa; for 15 species Fs had decreased two times or more. However, 14 of the markedly declined taxa, e.g. the long-term dominating submergent *Potamogeton perfoliatus*, belong still among the top 33 in the list. A significant ($\chi^2 = 11.8$; $p < 0.028$) change was observed in the species number of different frequency classes. The number of taxa in the Fs class 46–100 (92)% was 17 in 1970–1980 but only 3 in 1997–2007. The top of the list of macrophytes is dominated by circumpolar species and vicariants. Impoverishment of the flora in the course of eutrophication is expressed by the decrease in Fs; at the same time, the total number of species had not changed. Among the 20 declined taxa 14 are characteristic of the temporarily flooded and/or shallow-water zone of eutrophic water bodies (amphibious and emergent plants); the remaining taxa are shallow-water submergents. The simpliest explanation for their decrease is the expansion of thick reeds occupying suitable eulittoral habitats.

1. Introduction

Species richness of macrophytes is closely related to the natural type and status of a lake. Meso-eutrophic lakes are richer in species than oligotrophic or hypertrophic lakes (Rørslett, 1991; Andersson, 2001). As most submergent macrophytes, especially vascular plants, use bicarbonate ions as a source of carbon (Madsen and Sand-Jensen, 1991), hard-water lakes are usually more productive and richer in species than soft-watered–sandy bottom seepage lakes or genuine oligotrophic lakes. The poorest in submergent macrophytes are dystrophic and acidotrophic brown-water lakes (Maristo, 1941; Ott and Kõiv, 1999) or lakes lying on acidic bedrock and characterized by slow water exchange (Hunter et al., 1986; Rørslett, 1991; Mäkelä et al., 2004). In the course of anthropogenic eutrophication of oligotrophic lakes, enrichment with phosphorus and nitrogen may or may not be accompanied by an increase in alkalinity of water. In the former case also enrichment of the macrophyte composition with common species takes place, which suppresses mosses, isoetids and other characteristic inhabitants of these lakes (Mäemets, 1991). In Estonia lakes with HCO_3^- content over 80 mg L^{-1} are considered hard-water lakes and their lowest trophic status may be mesotrophic (Mäemets, 1974). As a rule, hard-water lakes with mean depth less than 3 m are naturally eutrophic. Some hard-water lakes with a relatively high depth/area ratio and without a distinctly limited hypolimnion were determined to be mesotrophic (Mäemets, 1974). However, the mesotrophic state is not clearly expressed through the characteristic macrophyte composition in small Estonian lakes owing to their steep slope and narrow littoral zone (Estonian database of macrophytes). The most characteristic vegetation of mesotrophic lakes, according to Interpretation Manual of European Union Habitats (1996), was found in the largest, unregulated Lake Peipsi, which has a shallow basin, sandy bottom and relatively long water retention time (Mäemets and Mäemets, 2001). In the mesotrophic state such lakes of northeastern Europe provide open (without tall emergents) shallow-water areas for several isoetids and small amphibious plants such as *Littorella uniflora* (L.) Asch., *Subularia aquatica* L., *Potamogeton gramineus* L., *Elatine hydropiper* L., *Eleocharis acicularis* (L.) Roem. et Schult, *Ranunculus reptans* L., etc. (Raspopov, 1985; Hellsten, 2000; Mäemets and Mäemets, 2001). One can suppose that the general increase in the trophic level of these lakes should also be reflected in the macrophyte composition.

Analysis of trends in the macrophyte diversity of large European lakes in recent decades is complicated. Despite excellent overviews

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for different lakes and periods (Raspopov, 1985; Schmieder, 1998; Andersson, 2001), summaries of changes in species richness are not available for worldwide use, or there are no comparable data for this purpose. The main aim of the present paper is to provide an analytical overview of changes in the macrophyte composition of L. Peipsi based on comparison of the frequencies of 67 taxa for the periods 1970–1980 and 1997–2007. For a better understanding of our results, some methodological issues have been treated here, the first being correlation between relative abundance and frequency. Another issue is inter-annual difference in species richness. Most investigators have had no possibility of studying one and the same lake every year, but the occurrence of several species may vary markedly over short periods owing to natural causes.

2. Materials and methods

2.1. Study site

The total area of L. Peipsi (lying on the border of Estonia and Russia) is 3555 km^2, mean depth 7.1 m, maximum depth 15.3 m. The longitudinal axis proceeds more or less from north to south. The coordinates of the lake are 57°51′–59°01′N; 26°57′–28°10′E. The bedrock of the lake basin consists mostly of Devonian sandstone, but in the northernmost and southernmost parts also outcrops of Ordovician and Devonian limestone are present, respectively. The volume of the whole lake is 25.1 km^3 at mean water level and the residence time of the water is about 2 years. The main inflows are the Velikaya River in the south and the Emajõgi River in the west; the outflow into the Gulf of Finland occurs via the Narva River. Water level is not regulated and its mean is 30 m a.s.l.; fluctuations are large, the average annual range being 1.15 m (Jaani, 1996). The basin includes four landscape regions (Fig. 1). The southern half – L. Lämmijärv (=L. Teploe) and L. Pihkva (=L. Pskov) – is bordered with the swampy and sparsely inhabited Peipsi Coastal Lowland. In the northernmost part the densely forested Alutaguse Lowland begins behind the high coastal dunes. The more densely inhabited Ugandi Plateau in the west and the Plyussa Plateau in the east extend to the shore of the lake's northern, largest part, L. Peipsi sensu stricto (=L. Chudskoe) (Karukäpp, 2008). The lake bottom is mainly formed of silty and

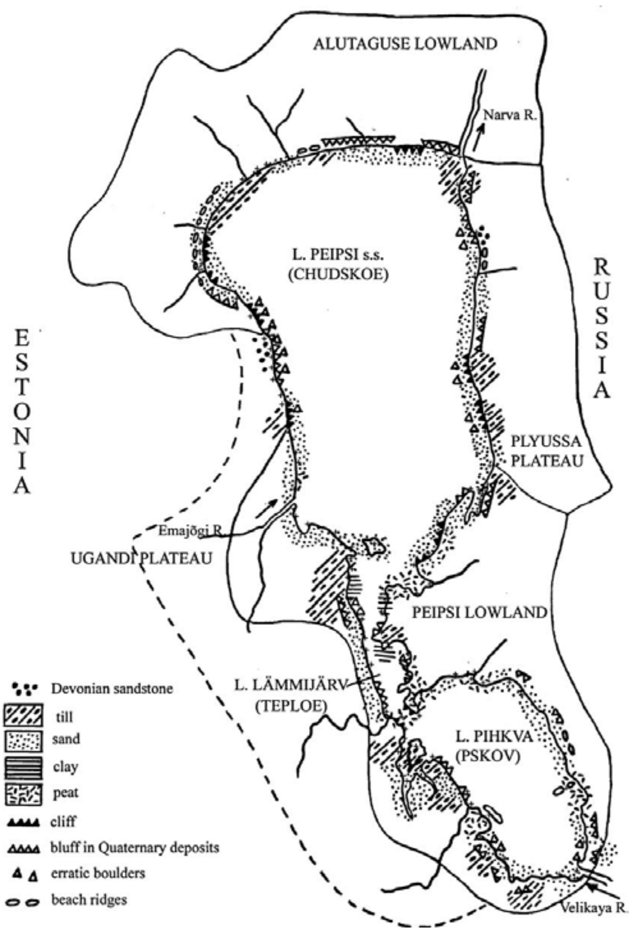

Fig. 1. Shore types of Lake Peipsi and the surrounding landscape regions; compiled on the basis of the maps by Tavast (2008) and Karukäpp (2008); + = our stations in 1997–2007.

sandy sediments; in some smaller areas also of clay or peat (Raukas, 1999). In deeper areas the content of organic matter in the mud layer accounts for $\leq$40% (Raukas, 2008).

A strong anthropogenic impact on the lake was reflected in large amounts of sodium, potassium, sulfate and chloride ions in its water already in the 1960s (Starast et al., 2001). Nevertheless, the northern part was considered to have mesotrophic features and the southern part to be eutrophic until the 1970s. Recently, the southernmost part of the lake (L. Pihkva), was considered hypertrophic, the northernmost part (L. Peipsi s.s.) eutrophic and L. Lämmijärv, close to hypertrophic (OECD, 1982; Kangur and Möls, 2008). An earlier comparable macrophyte dataset, compiled by Estonian botanists for 1970–1980, reflects the period of rapid changes in the lake's ecosystem; the dataset for 1997–2007 represents the already increased trophic level. Besides the increase in the availability of nutrients, strong water blooms of the cyanobacteria *Anabaena*, *Aphanizomenon* and *Microcystis* showed an increasing trend during the last decade (Laugaste et al., 2008), while filamentous green algae (mainly *Cladophora*, but also *Rhizoclonium* and *Ulothrix*) were abundant on many monitoring transects.

2.2. Earlier macrophyte data

The first data on the vegetation of the whole L. Peipsi were collected in 1962–1963 by Tuvikene (1966) and in 1966–1970 by Nedospasova (1974). Direct comparison of their data with the results of subsequent investigations is not possible as the estimates for the relative abundances of species were given separately for the three lake parts and on a 1–3-point scale by Tuvikene; and on a 1–4-point scale for the whole lake by Nedospasova. Information on the flora of the temporarily flooded zone was relatively scarce, and the number and location of the investigation stations is unknown. However, these datasets have been used here to reveal changes in the distribution of the species between the lake parts. The data by Nedospasova also provide preliminary estimation of the lake areas occupied by macrophytes and can be used to follow changes affecting reeds.

In the following investigations an 1–5-point scale was used to estimate the relative abundance of different taxa in the lake. Altogether 50 stations over the whole lake, with a distance of 10–11 km between them, were studied repeatedly in 1970 and 1980. Thirty-seven additional stations in different stretches were studied in the years 1970, 1971 and 1980. On the basis of the data from these 87 stations, the frequency (Fs) of 67 taxa, mainly hydrophytes, but also of the main emergent and amphibious plants, was calculated for each lake part and for the whole lake (Mäemets and Mäemets, 2001).

2.3. Data sampling

Our investigations were carried out in 1997–2007. The generalized relative abundance (As) of each species (in some cases genus) was estimated on a 1–5-point modified scale of Braun-Blanquet for every transect (station): 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 (emergents, submergents, etc.). The total number of investigated stations over the whole lake was 139, of these 57 stations were visited twice or more often. The total number of observations for all these stations in 1997–2007 was 243. Species composition and As were studied on the transects beginning from the upper boundary of the temporarily flooded zone to the deepest growth zone. However, some species characteristic of the dunes of L. Peipsi were included as well. The width of the transects was ca. 20 m on the shore and near the water's edge and ca. 10 m in deeper water. Although the vegetation of the boat canals and shore pools was included in the taxa list, the data for As and frequency calculations were not adequate for all the species. For repeatedly visited stations, the mean value of abundance over the years was calculated and all (single-year or averaged) transect/station relative abundances As1, As2, etc. were summarized as overall abundance (*A*). Frequency (Fs) was calculated for the stations over the whole lake as the percentage of the number of the stations where the species occurred of the total number of stations (139). Inter-annual differences were followed for 14 transects in 2005–2007. The Fs of the *Carex*, *Chara* and *Juncus* was compared with older Fs data (1970–1980) on the genus level, as earlier determination has been made only on this level. In recent investigations, the main species of the above three genera in L. Peipsi were *Carex acuta* L., *Chara contraria* A. Braun and *Juncus articulatus* L.

2.4. Statistical analysis

For statistical analysis, we used the procedures provided by the program R version 2.8.1 (R Development Core Team, 2008). For testing if frequencies for the earlier and for the recent periods had the same distribution, we used the Wilcoxon Signed Ranks test. To compare the proportions of each species, we tested statistically significant differences between the earlier and the recent data using the *z*-value (Freund and Wilson, 2003).

3. Results

3.1. Abiotic factors

The three parts of L. Peipsi (Fig. 1) differed in the trophy level also in the period of our study. The mean values of water chemical characteristics (in surface layer during the vegetation period) for the whole lake and its three parts are presented in Table 1. Both observed periods (1970–1980 and 1997–2007) include the years with very low water and high water, as well as warm and cold summers (Fig. 2).

Table 1
Main water characteristics of Lake Peipsi in 1997–2007.

Parameter[a]	Lake Peipsi			Part of the Lake Peipsi		
	Mean	95% tolerance limits		Peipsi s.s. (Chudskoe)	Lämmijärv (Teploe)	Pihkva (Pskov)
pH	8.37	7.79	9.00	8.36	8.35	8.65
Secchi depth (m)	1.39	0.59	3.20	1.7	0.96	0.72
PO_4^{3-} (mg P m^{-3})	15.6	1.2	61	7.1	11.5	28.22
$NO_3^- + NO_2^- + NH_4^+$ (mg N m^{-3})	100	38	250	97	100	101
HCO_3^- (mg L^{-1})	152.5	116.0	189.1	158.6	136.7	150.7
TP (mg P m^{-3})	51.7	17.4	154	41.7	80.5	126
TN (mg N m^{-3})	698	373	1307	632	856	1050

[a] Measured in surface water layer during the ice-free period.

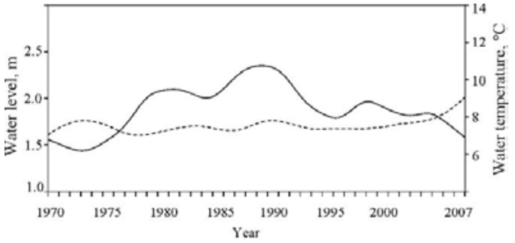

Fig. 2. Long-term changes of the mean annual water level (—) and water temperature (- - -) of Lake Peipsi (averaged and flattened), according to the daily data from the Estonian Meteorological and Hydrological Institute. Water level 2.0 m is equal to 30 m a.s.l.

3.2. Characteristics of macrophyte vegetation

The macrophyte list of the taxa of L. Peipsi for the period 1997–2007 consists of 140 species of vascular plants and bryophytes, and of 8 taxa of charophytes and large green and red algae. Higher plants were present by 3 species of dune plants, by 50 species of the temporarily flooded zone, by 47 emergent and amphibious plants, by 5 floating-leaved plants, by 6 floating plants and by 28 submerged plants. The number of species has not changed. Comparison of the periods 1962–1980 and 1997–2007 reveals the disappearance of two most sensitive species, *Isoëtes echinospora* Durieu (found in 1966–1970), and *S. aquatica* L. (found in 1962–1980), and the appearance of two new species, *Potamogeton praelongus* Wulfen (since the 1980s) and *Lemna gibba* L. (since 2006). Among all angiosperm species of L. Peipsi, 16 (11%) are on the border of their distribution. The taxa list of higher plants and charophytes is presented in Table 2. The littoral vegetation was the poorest on the shores formed of boulders, denuded sandstone or young dunes. The richest were stretches with the prevailing till shore (Fig. 1). The maximum depth at which submerged plants were registered in 1997–2007 was about 4 m, while the usual depth limit of denser stands of pondweeds was 1.5 m. The minimum and maximum species numbers per transect for the last decade (1 and 40), were similar to the corresponding figures for the period 1970–1980 (2 and 42). During the whole documented period *Phragmites australis* (Cav.) Trin. ex Steud. and *Potamogeton perfoliatus* L. have been the two dominating taxa in the whole lake. In recent decades earlier floristic peculiarities of the lake parts were levelled, as in the 1970s the growth areas of several nutrient-demanding species (Schmieder, 1998; G.-Toth et al., 2008) extended from the southern to the northern lake part, when there appeared *Zannichellia palustris* L., *Elodea canadensis* Michx., *Ranunculus circinatus* Sibth., *Ceratophyllum demersum* L., *Lemna trisulca* L., *Spirodela polyrhiza* (L.) Schleid. and *Potamogeton pusillus* L. (Tuvikene, 1966; Nedospasova, 1974; Mäemets and Mäemets, 2001).

3.3. Comparison of relative abundance and frequency

In Table 2 taxa are arranged according to the values of their Fs in 1997–2007. The table also presents the Fs of 67 taxa for 1970–1980 and their position numbers for the both periods. Calculation of the Fs for the period 1997–2007 is based on a larger dataset compared with the period 1970–1980. In the group of species with the highest frequency (Fs $> 20\%$), earlier Fs data for 1970–1980 were not available for four shore species: *Polygonum lapathifolium* (26%), *Stachys palustris* L. (26%), *Bidens tripartita* L. (25%) and *B. cernua* L. (21%). Hence it was not possible to judge the success or decline of these species. To study the relationship between abundance and frequency, we compared overall abundance (*A*) and frequency per stations (Fs). Correlation between *A* and Fs was significant (Rs = 0.93). Fig. 3 presents the first 33 species according to their Fs and *A* values using the same scale. The general order of the taxa according to Fs and *A* is relatively similar. Several larger differences obviously depend on the stand's character: some species usually form appreciable mats, others are frequent but more scattered.

3.4. Inter-annual variability

The appearance of seedlings of many species of the temporarily denuded shore in 2006 indicated the richness of the seed bank not expressed every year. However, the number of taxa per transect/station in 2005–2007 did not show any clear trend. Table 3 presents the data of five taxa growing near the water's edge. Their appearance obviously depended on the year. Decreasing water level and increasing water temperature in 2006–2007 (see also Fig. 2) caused an increase in *C. contraria*, *Potamogeton pectinatus* L., *R. reptans* L., *Alisma gramineum* Lej. and *Cyperus fuscus* L. The difference in Fs for 2005 and 2006 was statistically significant ($p < 0.05$) for all these species.

3.5. Long-term changes in frequency and the "top list" of compared datasets

The distribution of the Fs for the 67 taxa with available Fs data for the periods 1970–1980 and 1997–2007 was statistically different ($p < 0.03$). A statistically significant ($p < 0.05$) decline occurred in the case of 20 taxa, among them Fs decreased twofold for 15 species (Table 2). Despite its continuous domination among the submergents, *P. perfoliatus* too showed a statistically significant decline. Among the declined taxa 14 belong to the group of amphibious and emergent plants, and the rest to submergents. A significant ($\chi^2 = 11.8$; $p < 0.028$) change took place in the species number of different frequency classes. In 1970–1980 the group of species with the Fs of 47–100 (92) % included 17 taxa, while in 1997–2007 only 3 dominating taxa belonged to this Fs class. Several species in the Fs class of 11–46% in 1970–1980 belonged to the Fs class of 0–10% in 1997–2007 (Table 2). Out of 20 significantly declined taxa 13 dropped at least 10 places lower in the list in 1997–2007. In some cases the species of significantly declined Fs, e.g. *Butomus umbellatus* L. ($63\% \rightarrow 39\%$), retained their earlier position. Several species with a marked though not significant decrease in Fs even improved their positions, e.g. *Agrostis stolonifera* L. and *P. pectinatus* (Table 2). The position of some taxa improved to a great degree, e.g. *C. demersum* rose 20 places. Also *S. polyrhiza*, *Rumex maritimus* L., *Myriophyllum spicatum* L., *E. canadensis*, *E. acicularis* (L.) and *Juncus* spp. rose at least 10 positions.

4. Discussion

Considering that the accuracy of Fs depends only on correct determination of species, while As also depends on the experience and possible subjectivity of the investigator, use of Fs for expressing the importance of species in a large lake in the case of transect investigations is preferable. However, the correlation between these two characteristics will very probably decrease in the case of a smaller dataset. Comparison of the frequency per all observations and the frequency per all stations/transects (Fs, used here) suggest that the latter is a better indicator because repeatedly visited stations may increase the role of some species occurring there permanently. On the other hand, inter-annual fluctuations should not be neglected in case the vegetation of a lake is studied with an interval of several years or decades, as the conclusions based on a single season may prove erroneous.

Table 2
Macrophyte taxa of Lake Peipsi.

Order of taxa according to the Fs in 1997–2007	Fs in 1970–1980, %	Fs in 1997–2007, %	*A*	Ordination no. among 67 taxa in 1970–1980	Ordination no. among 65[a] taxa in 1997–2007
Phragmites australis	91	89	80.0	2	1
Potamogeton perfoliatus	92	75	63.6	1	2
Carex spp. (incl. determined species)	54	48	26.6	10	3
Alisma plantago-aquatica L.	39	45	19.2	20	4
Agrostis stolonifera	51	44	24.2	13	5–7
Sium latifolium L.	60	44	18.3	8	5–7
Potamogeton pectinatus	51	44	37.0	14	5–7
Schoenoplectus lacustris	90	43	30.8	3	8
Sagittaria sagittifolia	78	40	25.6	4	9
Butomus umbellatus	63	38	19.1	7	10
Eleocharis acicularis	45	37	30.3	18	11
Rorippa amphibia (L.) Besser	31	36	13.0	23–24	12–13
Elodea canadensis	31	36	23.2	23–24	12–13
Glyceria maxima	47	35	17.6	16–17	14
Polygonum amphibium L.	72	31	9.5	6	15–18
Myriophyllum spicatum	30	31	17.9	25–26	15–18
Phalaris arundinacea L.	15	31	14.7	37–39	15–18
Juncus spp. (incl. determined species)	15	31	10.0	37–39	15–18
Eleocharis palustris (L.) Roem. et Schult.	74	30	25.1	5	19
Rumex maritimus	11	28	10.9	43–47	20
Alisma gramineum	53	27	28.9	11	21
Stachys palustris		27	11.8		
Lythrum salicaria	32	26	12.8	22	22–23
Polygonum lapathifolium		26	16.2		
Potamogeton gramineus	60	26	14.9	9	22–23
Nuphar lutea (L.) Sm.	29	25	10.7	27	24
Equisetum fluviatile	51	24	15.0	15	25–27
Ranunculus reptans	52	24	13.2	12	25–27
Lemna trisulca L.	25	24	14.2	30	25–27
Typha latifolia L.	16	23	6.3	35–36	28–29
Chara (*Ch. contraria*, *Ch. aspera* Deth. ex Willd.)	47	23	18.6	16–17	28–29
Iso- and Hypnobryales (mainly *Fontinalis antipyretica* Hedw.)	23	22	7.6	33	30
Lycopus europaeus L.		20	8.5		
Stratiotes aloides L.	28	20	12.0	28–29	31
Ceratophyllum demersum	3	19	10.7	57–60	32–33
Eleocharis sp. (hybrids?)		19	4.3		
Hydrocharis morsus-ranae L.	11	19	7.1	43–47	32–33
Bidens tripartita		18	3.5		
Spirodela polyrhiza	10	18	12.5	48–49	34
Bidens cernua		17	7.0		
Sagina nodosa (L).Fenzl.		17	3.6		
Lemna minor L.	11	17	5.6	43–47	35
Galium palustre L.		16	4.2		
Myosoton aquaticum (L.) Moench		16	8.0		
Carex acuta		15	11.7		
Achillea salicifolia Besser		14	7.6		
Cicuta virosa L.		14	3.5		
Lysimachia vulgaris L.		14	6.7		
Myosotis scorpioides L.		14	4.8		
Ranunculus sceleratus L.		14	2.9		
Sparganium emersum	24	14	11.2	31–32	36
Typha angustifolia L.	30	13	6.3	26	37
Scolochloa festucacea (Willd.) Link	24	12	8.0	31–32	38–40
Epilobium palustre L.		12	3.9		
Ranunculus circinatus	11	12	6.5	43–47	38–40
Sparganium erectum coll.	14	12	3.8	40	38–40
Acorus calamus L.	40	11	7.3	19	41–43
Cyperus fuscus		11	4.4		
Eleocharis uniglumis (Link) Schult.		11	6.2		
Potamogeton lucens L.	11	11	6.5	43–47	41–43
Zannichellia palustris	16	11	6.3	35–36	41–43
Iris pseudacorus L.		10	4.8		
Mentha arvensis L.		10	7.1		
Petasites spurius (Retz.) Rchb.		10	6.9		
Nymphaea spp. (mainly *N. candida* C. Presl.)	7	9	3.4	51	44
Symphytum officinale L.		9	3.9		
Scirpus radicans	10	8	3.1	48–49	45–46
Solanum dulcamara L.		8	2.9		
Myriophyllum verticillatum L.	1	8	5.1	62–67	45–46
Alopecurus aequalis Sobol.		7			
Juncus articulatus		7	3.4		
Oenanthe aquatica (L.) Poir.	13	7	5.6	41–42	47–48
Scutellaria galericulata L.		7	2.5		
Elatine hydropiper	8	7	6.8	50	47–48

Table 2 (*Continued*)

Order of taxa according to the Fs in 1997–2007	Fs in 1970–1980, %	Fs in 1997–2007, %	*A*	Ordination no. among 67 taxa in 1970–1980	Ordination no. among 65[a] taxa in 1997–2007
Euphrasia officinalis coll. L.		7	2.7		
Calamagrostis canescens (Weber) Roth.		6	4.1		
Glyceria fluitans (L.) R. Br.	13	6	1.0	41–42	49–51
Juncus bufonius L.		6			
Ranunculus lingua L.	3	6	5.0	57–60	49–51
Bidens radiata		6	1.4		
Caltha palustris L.		6	3.7		
Epilobium hirsutum L.		6	2.1		
Rorippa palustris (L.) Besser.		6	2.4		
Potamogeton berchtoldii Fieber		6	3.3		
Utricularia vulgaris L.	1	6		62–67	49–51
Lysimachia thyrsiflora L.		5	2.5		
Rumex hydrolapathum	34	5	1.0	21	52–56
Potamogeton filiformis Pers.	15	5	1.6	37–39	52–56
Potamogeton pusillus	23	5	2.5	33–34	52–56
Potamogeton trichoides Cham. et Schltdl.	1	5	1.5	62–67	52–56
Nitella spp. (incl.) *Nitella syncarpa* (Thuill.) Cheval.	6	5		52–53	52–56
Calystegia sepium (L.) R. Br.		4	2.2		
Leymus arenarius (L.) Hochst.		4			
Galium aparine L.		4	1.0		
Inula britannica L.		4	0.8		
Stellaria palustris Retz.		4	2.2		
Potamogeton friesii Rupr.	2	4	1.1	61	57–58
Ranunculus trichophyllus Chaix	28	4	0.9	28–29	57–58
Potentilla palustris (L.) Scop.		3	2.7		
Epipactis palustris (L.) Crantz.		3	0.5		
Mentha × *verticillata* L.		3	0.9		
Senecio paludosus L.		3	2.0		
Nuphar pumila (Timm) DC.	6	3	1.0	52–53	59–61
Potamogeton crispus L.	1	3	0.6	62–67	59–61
Potamogeton natans L.	3	3		57–60	59–61
Ricciocarpus natans (L.) Corda		3			
Calamagrostis purpurea (Trin.) Trin.		2	1.0		
Equisetum palustre L.		2	0.5		
Lathyrus maritimus (L.) Bigelow		2			
Mentha aquatica L.		2	0.5		
Polygonum hydropiper L.		2	0.5		
Ranunculus repens L.		2	0.4		
Lemna gibba		2	2.0		
Nitellopsis obtusa Desv.		2	0.8		
Potamogeton compressus L.	3	2	0.2	57–60	62–63
Potamogeton obtusifolius Mert. et Koch	1	2	2.3	62–67	62–63
Carex vulpina L.		1	0.2		
Cladium mariscus (L.) Pohl		1			
Lathyrus palustris L.		1	0.3		
Menyanthes trifoliata L.		1	1.0		
Odontites litoralis Fr.		1	0.3		
Pedicularis palustris L.		1	0.5		
Thelypteris palustris Schott.		1	0.5		
Potamogeton acutifolius Link		1			
Potamogeton praelongus		1			
Potamogeton rutilus Wolfg.	5	1	0.1	54–56	64–65
Potamogeton × *suecicus* Richt.	5	1		54–56	64–65
Hottonia palustris L.		1			
Limosella aquatica L.		1			
Ranunculus eradictatus (Laest.) Nevski		1			
Carex aquatilis Wahlenb[b]					
Carex diandra Schrank[b]					
Carex elata Bell. ex All.[b]					
Carex hirta L.[b]					
Carex riparia Curtis[b]					
Carex rostrata Stokes[b]					
Chenopodium rubrum L.[b]					
Potentilla anserina L.[b]					
Thalictrum flavum L.[b]					
Juncus conglomeratus L.[b]					
Juncus effusus L.[b]					
Juncus filiformis L.[b]					
Juncus gerardii Loisel.[b]					
Juncus nodulosus Wahlenb.[b]					

In bold: significant decrease in Fs.

[a] *Subularia aquatica* and *Ranunculus aquatilis* were not found in 1997–2007.

[b] Data not adequate for the calculation of the Fs.

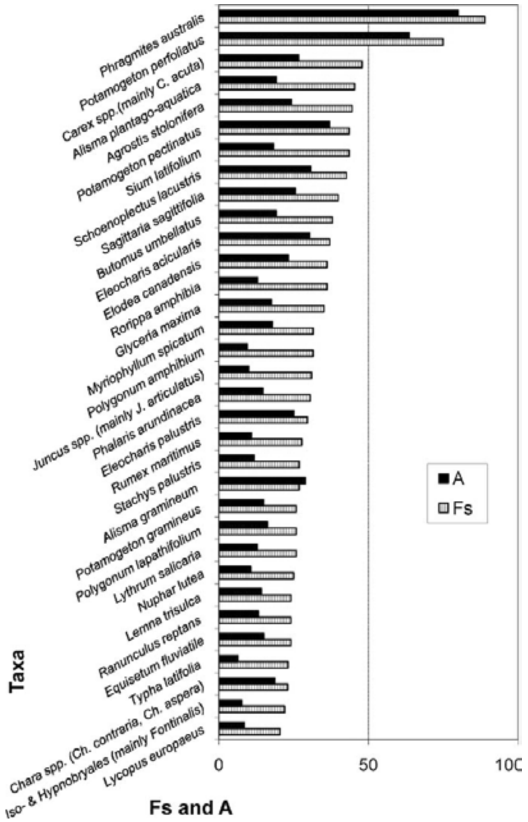

Fig. 3. The first 33 species according to the frequency per stations (Fs) and their summarized mean abundances (*A*) in 1997–2007.

Can a decrease in Fs indeed have taken place? Earlier calculations of Fs (87 stations) were based on a smaller dataset than the recent one (139 stations). So, although in the later investigations the probability of finding a species was higher, contrary trend in Fs was observed for many taxa. This suggests that the decreased Fs reflects the real situation in the lake. As we had data of many repeated observations at our disposal, the impact of inter-annual fluctuations should have been weaker than in the case a dataset based on single-year observations had been used.

Using available literature data on the species that have declined in L. Peipsi (Palmer, 1992; Preston and Croft, 1997; Schmieder, 1998; G.-Toth et al., 2008) we do not give for them a similar ecological characterization. Some are plants of mesotrophic water bodies with a sandy bottom, such as, e.g. *P. gramineus* L. and *R. reptans*, but most are inhabitants of eutrophic lakes, e.g. *Sagittaria sagittifolia* L., *P. perfoliatus*, *Sparganium emersum* Rehmann, *Rumex hydrolapathum* Huds., *B. umbellatus.* Also the Fs of macrophytes with a very wide ecological amplitude, e.g. *Equisetum fluviatile* L., was lower in the last decade. Plant size among the group of declined species is highly variable, from tall emergents to the smallest amphibious plants. The most evident reason for the decrease in Fs seems to be the occupation of the littoral by reeds, which has been the most significant change in the macrophyte vegetation in recent decades. In L. Peipsi an expansion of reeds towards the northern, earlier mesotrophic, part of the lake, and an increase in their density have been observed since the 1960s (Mäemets and Freiberg, 2004). The depth limit of reeds (as well as of other macrophytes) depends on water level; in most cases it is about 1 m. The width of reed stands in the northernmost part of L. Peipsi is 20–40 m, in the southern part the reed belt may be up to 1000 m wide, but usually it is 150–300 m. The number of fresh reed shoots per square meter which was 30–150, depended on the site and on clone characteristics; the average height of fertile reed shoots was 296.7 ± 67.6 cm on the Estonian shore in 2001–2002 (Mäemets and Freiberg, 2004). Also dense stands (up to 200 shoots per m^{-2}) of *Schoenoplectus lacustris* (L.) Palla are characteristic of the southern lake parts.

Table 3
Frequency (%) of some eulittoral species in 14 stations of Lake Peipsi in 2005–2007.

Species	2005	2006	2007
Alisma gramineum[a]	14	64	43
Cyperus fuscus[a]	0	36	21
Chara contraria	14	57	43
Ranunculus reptans	7	29	29
Potamogeton pectinatus	29	86	64

[a] Species that are under nature protection in Estonia.

P. australis is a strong competitor forming pure stands in many places. The impact of the lake's eutrophication is mediated through reed, and the consequences of this process seem to be quite analogous to the result of fertilization experiments on grasslands, where addition of nutrients favored the decrease in species number and the prevalence of large-sized graminaceous species (Willems et al., 1993; Foster and Gross, 1998; Stevens and Carson, 1999). However, to increase species richness using chemical extinction of reeds, as is recommended by some authors (Garnett, 2002) and has been applied in some countries, is absolutely unacceptable due to the toxic effects of this procedure (not tested adequately) on different groups of the biota and on the ecosystem of the wetland as a whole (Blackbaum and Boutin, 2003; Lajmanovich et al., 2003). Also there arises the question about the proportion of extinction. According to our experience, the richest in macrophyte species are till shore stretches with different habitats, including reed stands of moderate size. The expansion of reeds may be temporal. In recent years in the hypertrophic southern part of L. Peipsi showed the first obvious signs that reed increase has stopped: in some stretches the stands had decreased and the mean biomass has slightly declined in comparison with 1988–1989.

Our dataset covers the period when species richness depended largely on human activity. Numerous boat canals had to be dug because of neotectonic transgression in the northern lake part and the expansion of reeds. Mounds of excavated sediments form sheltered areas for tall emergents, with reed growing closest to the lake. On the other hand, new or recently dredged canals and pools are inhabited by small-sized rare and declining species. Older, non-dredged canals with a mud bottom are favorable for nutrient-demanding species such as *C. demersum*, *S. polyrhiza*, etc. Thus, the lake offers littoral habitats of two types: open areas and canal areas.

Among the 20 declined taxa, 14 still belong to the first 33 in the list. Of the recently most frequent 33 species of L. Peipsi, 19 belong to the circumpolar floristic element (Preston and Croft, 1997; Kukk, 1999). Four of the most frequent species are invasive, having spread from Eurasia to North America (*M. spicatum*, *Lythrum salicaria* L., *Glyceria maxima* (Hartm.) Holmb.) or from North America to Eurasia (*E. canadensis*). Additionally, two Euro-Siberian species have vicariant species/subspecies in North America (*S. sagittifolia*/*latifolia*, *rigida*, *Nuphar lutea*/*advena*). About two-thirds of the main species, i.e. 19 species, are common for all nine large lakes of the northwestern part of the Russian Plateau (Raspopov, 1985). Obviously, cosmopolitan taxa are prevailing.

The flora of L. Peipsi is rich even today when eutrophication is seriously harming its ecosystem. One reason for this may be the location of the lake on the floristic border between the West and the East. The list of the taxa of the European largest lake, Ladoga (area 18,134 km^2 with islands; mean depth 50.6 m), contains 107 species of vascular plants represented as associations of hydrophytes, pleustophytes helophytes and hygrophytes (Raspopov, 1985). Lake Ladoga, situated about 250 km NE of L. Peipsi, has 23 plant species that have never been found in L. Peipsi. The 140 vascular plant species of L. Peipsi obviously include more species of the shallow temporarily flooded zone than occur in L. Ladoga whose northern shore is formed of fjords. As the water table of L. Peipsi is not regulated, favorable areas for the spreading of various hygrophytes, helophytes and hydrophytes develop there at least once per decade. On the other hand, some plants characteristic of the coasts of L. Peipsi and the Baltic Sea are not represented in the flora of L. Ladoga. The flora of the large very shallow Lake Võrtsjärv (270 km^2; mean depth 2.8 m), located about 80 km SW of L. Peipsi, contains 114 species which all occur also in L. Peipsi. At the same time, L. Peipsi is the main habitat for several rare species such as *C. fuscus*, *A. gramineum*, *E. hydropiper* L., *Bidens radiata* Thuill., *Scirpus radicans* Schkuhr, etc. Comparison of the flora of L. Peipsi with the checklist of Estonian freshwater macrophytes (compiled by L. Freiberg and H. Mäemets) reveals that the species of L. Peipsi account for 70% of the vascular plants in the checklist. However, impoverishment expressed by the decrease in the frequency of an appreciable number of species may lead to new cases of extinction.

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II

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A comparative study of macrophyte species richness in differently managed shore stretches of Lake Peipsi

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ABSTRACT

We have compared the floristic composition of managed (M) and wild (W) shore areas in the northwestern, eutrophic part of Lake Peipsi (3555 km^2, with unregulated water levels). Management techniques include uprooting or cutting of reeds and willows, building a terraced area between the dunes and the water edge and frequent mowing. In 2006 and 2008, macrophyte species richness was registered summarily for different shore stretches; in 2009–2010, a study on 12 transects, each with 10–15 quadrats of 0.5 m × 0.5 m, was carried out in the same area. In parallel to this, the vegetation in an overgrown inlet near the lake was studied. The aims were: (1) to estimate species richness on managed and wild shore areas and to determine the suitability of managed areas for maintaining declining species and (2) to study the impact of terrace building and duration of management on the vegetation.

In total, 116 herbaceous species were found during the study period. Xero-, meso- and hygrophilous apophytes were characteristic for M (managed) stretches and hydrophilous apophytes for W (wild) stretches. Small threatened amphibious plants and hygrophytes such as *Alisma gramineum*, *Ranunculus reptans*, *Sagina nodosa*, *Cyperus fuscus*, *Eleocharis* spp., *Juncus* spp. were characteristic for the M stretches. The number of species was the highest (average per quadrat 11) in the mowed intermediate zone between the terrace and open water. In the inlet area the number of protected plants was highest in the first study year (2006) and then declined from 5 to 2. The highest total number of species was found in areas under ownership with diverse M and W habitats. Jaccard's similarity coefficients (JSCs) for the whole study area between the years were 0.30–0.50. The calculation of 462 JSCs among all ownerships and transects for the study period yielded floristic similarities of 0–0.59. The year along with style of management seemed to have strongest relationship with higher JSCs, and the yearly changing water levels the most obvious reason for the changes. This study has revealed the contribution of active management towards the support of persistent species richness in conditions of changing water levels, but probably not supporting richness at the more stable water edge.

Introduction

Fresh water makes up only 0.01% of the world's water, but this tiny fraction of global water supports at least 100,000 species (Dudgeon et al. 2006). Declines in biodiversity appear to be far greater in fresh waters than in most affected terrestrial ecosystems (Sala et al. 2000). The decrease in species richness of wetlands is a worldwide concern, so to survey present and possible future changes are of fundamental importance. How biodiversity-ecosystem functioning in multispecies systems responds to stressors is still far from clear (Woodward 2009). Shores of the water bodies with remarkably changing water level are permanently affected by intermediate disturbance. This kind of disturbance maintains highest level of diversity (Connell 1978). Some stressors may be mediated by natural factors. In boreal areas increasing trophic levels of shallow water bodies may enhance the dominance of cosmopolitan species with large genetic variabilities, *e.g.*, helophytes, and at the transition from oligo-mesotrophic to eutrophic conditions, there is often an expansion of the common reed *Phragmites australis* (Cav.) Trin. ex Steud. subsp. *australis* (Mäemets and Freiberg 2004; Čížková and Kvet 2009; Liira et al. 2010). During the last few decades, a significant decline in the frequency of several macrophyte species has been observed in the large, shallow eutrophic Lake Peipsi in Estonia, and the most probable reason for this decrease is the expansion of thick reed areas occupying suitable eulittoral habitats (Mäemets et al. 2010). The factors favouring the success of the reed are the presence of non-regulated, highly changeable water levels and transitions from mesotrophic to eutrophic conditions, such as have taken place in the large northern part of Lake Peipsi. Such conditions are favourable for the reed expansion, within a general background of reed declines in numerous highly eutrophic and regulated

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waterbodies in Europe (summarized by Čížková and Kvet 2009). Among the protected and other declining taxa of L. Peipsi are small-sized amphibious plants and hygrophytes such as *Alisma gramineum* Lej., *Ranunculus reptans* L., *Sagina nodosa* (L.) Fenzl, *Cyperus fuscus* L., *Eleocharis uniglumis* (Link) Schult. *Juncus articulatus* L., *J. gerardii* Loisel., *J. nodulosus* Wahlenb., and *Potamogeton gramineus* L.; however, there are also decreases in medium-sized helophytes such as *Eleocharis palustris* (L.) Roem. et Schult. and submerged plants such as *Chara contraria* A. Braun and *Potamogeton perfoliatus* L. (Mäemets et al. 2010). Some studies have documented the negative effects of reed cutting on wildlife, including macrophytes, invertebrate communities and passerine birds (Farnsworth and Meyerson 1999; Valkama et al. 2008). On the other hand, Cowie et al. (1992) found that cutting of reeds positively affected floristic diversity in the undergrowth of wetlands. Reed bed management can slow down or even reverse succession, so that a balance of different habitat types can be maintained (Hawke and Jose 1996). All these studies reveal that a moderate level of human impact (intermediate disturbance discussed by Connell 1978) can have positive effects on biodiversity.

Local people and holidaymakers near Lake Peipsi are interested in having open shores without reed beds. The aim of the lakeshore management has been to prevent any undesired spread of tall and thick reed stands. Unfortunately, this kind of activity was planned and organized by local residents who have little knowledge about possible effects on other macrophytes growing in this environment. Only a limited amount of information is available about the consequences of reed removal on changing the real floristic composition in managed, as compared with unmanaged, shore stretches. In this study we have compared species richness on managed and unmanaged shore areas over several years, and also compared species diversity on differently managed shore stretches. The specific objectives of the study were to: (1) reveal species richness and composition on managed and wild shore areas and the suitability of managed areas for species in decline and (2) study the impact of terrace building and duration of management to the vegetation.

Table 1

Selected water characteristics: dissolved inorganic nitrogen (DIN), total nitrogen (TN), phosphate (PO_4^{3-}), total phosphorus (TP), bicarbonate (HCO_3^-), pH and Secchi depth of Lake Peipsi s.s. in 1997–2010, presented as geometric mean values with 95% tolerance limits for the open water period (Julian days 100–310 for each year). Data were obtained from the database of the State Monitoring of Lake Peipsi.

Parameter	Number of measurements	Mean	95% tolerance limits	
DIN ($mg\,N\,m^{-3}$)	544	118.2	31.4	445.0
TN ($mg\,N\,m^{-3}$)	543	729.9	392.6	1356.9
PO_4^{3-} ($mg\,P\,m^{-3}$)	542	8.0	1.2	52.9
TP ($mg\,P\,m^{-3}$)	543	47.5	15.8	143.3
HCO_3^- ($mg\,l^{-1}$)	543	151.8	120.4	191.5
pH	481	8.4	7.7	9.0
Secchi depth (m)	558	1.6	0.3	2.8

Materials and methods

Site description

Lake Peipsi on the border between Estonia and Russia is one of the largest lakes in Europe. Its total area is 3555 km^2, mean depth 7.1 m and maximum depth 15.3 m. Main inflows are the Velikaya River in the south and the Emajõgi River in the west. The water level is unregulated; average annual fluctuation of the water level during the period 1890–2005 was 1.5 m and its absolute range was 3 m (Jaani et al. 2008). Mean values for the chemical composition of the surface water are presented in Table 1. As in many shallow lakes in Europe, eutrophication is the most serious problem for Lake Peipsi (Kangur and Möls 2008). The ecological state of the lake is also strongly influenced by natural processes, among which periodic fluctuations in water level and temperature are the most important (Kangur et al. 2003).

Our study area is situated in the northwestern part of Lake Peipsi at Vilusi village (Fig. 1). Species composition was studied in August 2006 at extremely low water levels, in September 2008 with rising water levels, and at high water in the July-August period in 2009

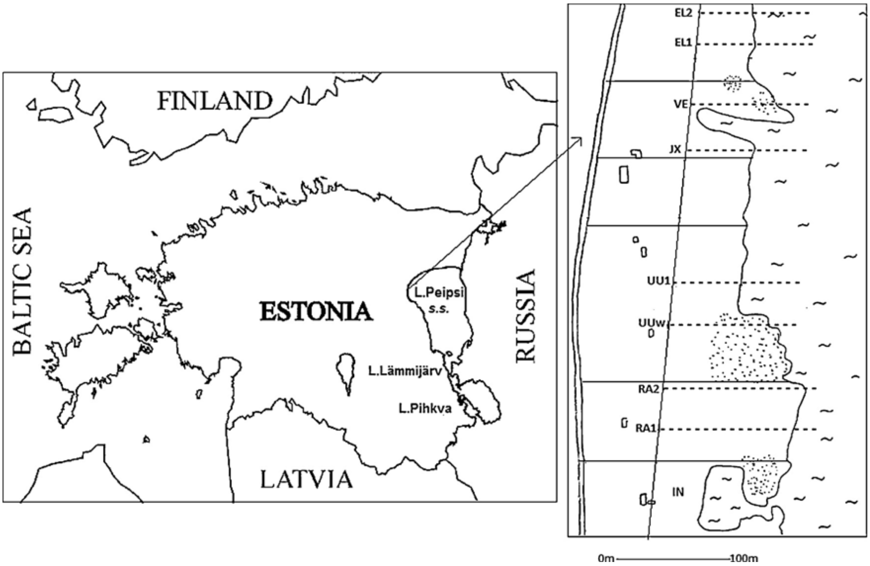

Fig. 1. Location of Lake Peipsi with a schematic drawing of the northern portion of the transects used and the inlet (IN). Abbreviations represent the owners of different transects measured. Conventional signs: ══ – road; □ – buildings; ∷ – reed and willows; ~ – water; – – property boundaries.

Table 2
Shore stretches studied and number of transects in the years 2006–2010. RA, VE, *etc.*, are abbreviations of the names of stretch owners.

Shore stretch	RA	VE	JX	UU[a]	EL	AJ	PA	SL[a]
Year of the bulldozer work	1999	?	1993	2008	2006	Not made	2004	2004
2006 Property study	x			x	x			
2008 Property study	x	x	x	x	x			
2009 Transect study	2	1	1	2	2		1	2
2010 Transect study	2	1	1	2	2	1	1	2

[a] One of the two transects was located in the remaining wild portion of the owner's land.

and 2010 (Fig. 2). Data for the water levels were obtained from Estonian Institute of Meteorology and Hydrology. The water level in the spring of 2010 rose to values comparable with the highest ever measured since 1922 (Jaani et al. 2008). Thus, the study period covered remarkable increases in water levels and the shore area became up to 30 m narrower in 2010 than in 2009.

Information about the management techniques, time and extent was obtained from local residents by questionnaires about every studied property (8). In addition, personal communications took place during the fieldworks to specify extra information.

Lake Peipsi is rich in macrophytes and the list of plant taxa includes 140 species of higher plants and 4 charophytes (Mäemets et al. 2010). Our study site has a flat till shore and belongs to the group of most species-rich lake areas with respect to macrophytes. According to local people, *P. australis* appeared in this area in the 1970s and started to spread along with rapid eutrophication in the 1980s. Reed beds presently extend from the shore for about 100 m, but between the thick, tall lakeside reed and the shore grow willows and/or sedges; in some places there are also *Glyceria maxima* (Hartm.) Holmb. and *Equisetum fluviatile* L. Turf layer, found in several marine coastal reedbeds (Sammul et al. 2011), is not formed at our study site. The shore area investigated was located between a border of dry dunes and a shallow littoral zone, to a water depth of 0.5 m in 2006 and 2008 and of 0.6–0.8 m in 2009–2010. The earliest reed removal in the study area took place in 1993, the most recent in 2008 (Table 2). The main scheme of management (this is not legislated) has been: (1) uprooting of reed, willows and other tall plants using a bulldozer; (2) sampling and burning of this material and (3) pushing the sand (and other mineral sediments) up the shore and building a terraced area between the dunes and the water edge. After these works, about every 2–4 weeks mowing is usually carried out between the months of May and September. However, for several reasons some patches of managed stretches remained unmown for some months. According to the local people, the success of reed removal essentially depends on the slope of the terrace formed. As the water level in Lake Peipsi changes continuously, in high water years this terrace might be destroyed by waves.

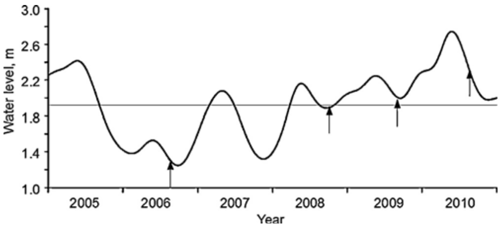

Fig. 2. Water levels during the study years; base lines for comparison are the long-term mean and benchmark value of 28 m abs (data from Tiirikoja Meteorological Station). Arrows are indicating the positions of the sampling dates.

Field work and data collection

In 2006 and 2008, all shore taxa in the different properties were registered as a total number ('property study'). In 2009 and 2010, more detailed transect investigations using 0.5 m × 0.5 m quadrats with intervals of 9.5 m in the different properties were carried out. For transects (Fig. 1), GPS coordinates and landmarks for the first quadrat in each property were fixed. The northernmost transect started at N 58°52.39 E 26°57.29 and the southernmost at N 58°52.27, E 26°57.20. The number of transects was 11 in 2009 and 12 in 2010, and they were placed, depending of the width of the property, at distances of 30 m when located on the same property (Table 2). Altogether three wild (W) stretches were studied: two in parallel with managed (M) stretches belonging to the same owner and one other (in 2010). Most of the managed areas consisted of the following zones: (a) mowed terrace; (b) intermediate area and (c) water. Two managed areas were different from the others – one without terrace (EL) and the second with wide intermediate area and remains of old boat canal (SL). The total number of studied quadrats was 124 in 2009 and 135 in 2010; the number of quadrats per transect was 10–15, *i.e.*, the width of a study area was 100–150 m from dune edge up to a water depth of 0.6 m in 2009 and 0.8 m in 2010. Quadrats were divided into groups using the following parameters: (a) terrace, intermediate zone, water; (b) mowed/not mowed in this season (in managed areas)/wild (not managed at least 10 years) and (c) open water or water in the shadow of taller emergent plants or willows. Coverage (C) estimations of all taxa were recorded, and for quadrats with dense, overlapping plants, the sum of coverage estimations exceeded 100%. Coverage consisting of a few small shoots of a species was recorded as 1%. Coverage of the moss layer was estimated for the land quadrats, and the abundance of large filamentous algae was estimated using the scale of Braun-Blanquet, numbers 1–5 (Poore 1955) for the water quadrats, and also water depth was registered. For the shore stretches frequencies (*F*) of taxa were calculated. Due to possible effects caused by inexact determinations, *Carex, Eleocharis, Juncus, etc.*, were compared at genus level. The years 2006–2010 were used for *F* determinations.

There were 22 observations of managed stretches (4 property studies + 18 transects) compared with 7 observations of wild stretches (2 property studies + 5 transects). Excluded were taxa which were found to differ between F_W and F_M less than two fold and also those with low find numbers such as 0–1, 0–2, and 1–2. Coverage estimations were summarized for managed and wild sites in 2009–2010. Sensitivity to human impact of a species was attributed according to the method of Kukk (1999). Apophytes are synanthropic plants, favoured by disturbed habitats and hemeradiaphors are neutral to human impact. Ecological divison (xero-, meso-, hygro- and hydrophilous) of taxa was described according to the need of water supply (Usher 1996). Xerophilous plants tolerate a dry habitat, mesophilous occurring in the places where the water supply is neither scanty nor abundant, hygrophilous living in a plentiful supply of water and hydrophilous living in water. Seven protected plant species were found in our area. In

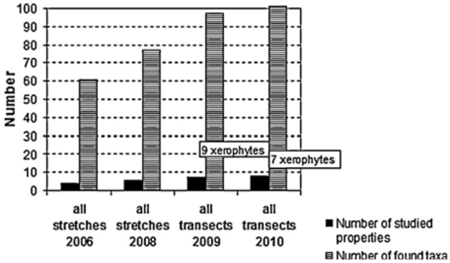

Fig. 3. Total number of properties studied and macrophyte taxa recorded on shore stretches in different years of the investigation.

addition to these, attention was also paid to the 19 species which are not listed as protected but have been observed to be declining in Lake Peipsi (see also Section 1).

In parallel to these studies, succession in the vegetation in one overgrowing inlet (width 30 m, length 60 m) was studied. The inlet is connected to the lake by a boat canal and it was deepened to 2 m depth in 2004.

Statistical analysis

Difference in ecological division of the taxa between the managed and wild shore stretches was tested using the Chi-Square test (Plackett 1983). Comparisons of frequency between managed and wild areas for each taxa was made using proportional analysis (*Z*-test). An analysis of floristic similarity among all the managed and wild stretches (2006, 2008) and transects (2009–2010) was carried out using the Jaccard's similarity coefficients. For this purpose 31 stretches/transects were compared by their pairs and then clustered by Ward's method (Ward 1963) on the basis of $JSC = C/(A + B - C)$, where A and B are species number in samples and C is the number of species shared by the two samples. The criterion for statistical significance was set at the 5% level. Statistical analyses were run in R 2.10.1 (R Development Core Team 2009).

Results

As water level rose remarkably during the study period (reaching in the spring of 2010 to the upper quadrats), the number of water quadrats was 50 in 2009 and 75 in 2010. 18 taxa were recorded only at genus level (*Salix*, mowed *Eleocharis*, *Juncus*, Carex, as well as some unidentified seedlings and other small specimens). In some cases mowed *Poaceae* were classified only at family level, and relatively scarce tiny mosses under the vascular plants remained unidentified in all shore quadrats.

During the study years 116 plant species were found, among them nine were found only in the inlet. The total number of macrophyte taxa yielded in the property studies was 61 in 2006 and 77 in 2008; in the transects, 97 in 2009 and 101 in 2010 (Fig. 3). The results for the transect studies did not exceed significantly the numbers found in the property studies when considering the number of hygrophyte (moisture-demanding) and hydrophyte species and the larger number of properties included for the 2009–2010 analyses. In the summer of 2010 mesophytes were found in quadrats 10–20 m further up the shore than in 2009. In 2009 large filamentous algae (mainly *Cladophora*) were found in three transects but in 2010 they were in 10 transects and in larger quantities.

Species composition and coverage on managed and wild shore areas

Statistical analysis (Chi-Square test) has revealed that the ecological division of taxa is different for managed and wild stretches. Putting all the data from all years together, 37 taxa were found only on managed and 8 only on wild stretches, and 59 taxa were present in both types of stretches (JSC = 0.57). Ecological division of: (a) taxa present only on managed or at least twofold higher *F* levels on managed stretches; (b) analogous taxa for wild stretches (Fig. 4) reveals that there are more groups on managed areas. All of the xerophytes and a larger proportion of the mesophytes were present only on managed areas (in regions mostly elevated by bulldozing). The proportion of apophytes was slightly higher on managed than on wild stretches, but apophytic *Glyceria maxima*, *Lemna minor* L., *L. trisulca* L. and *Spirodela polyrhiza* (L.) Schleid. were found mainly in the wild areas. Small-sized and declining amphibious plants and hygrophytes such as *A. gramineum*, *R. reptans*, *S. nodosa*, *C. fuscus*, *Eleocharis* spp., and *Juncus* spp. were characteristic of managed stretches (Table 3). In addition, submersed macrophytes were more frequent in the open water of managed stretches, as compared with wild stretches, but *Utricularia vulgaris* L. and *Myriophyllum verticillatum* L. were found only in the shaded water quadrats of wild areas. *P. gramineus, P. perfoliatus*, *Myrophyllum spicatum* L. and *Zannichellia palustris* L. were found only in open water and the last two only in managed areas. However, the presence or absence of some species in decline was not correlated with the management regime of the land.

Within different zones the overall average number of species per quadrat decreased going towards the water: 9, 8 and 4 species, respectively. Comparison of quadrats with different characteristics (according to zone, mowing, open water or shaded) revealed the highest number of species in the mowed intermediate zone (average number per quadrat = 11, and in the mowed terrace = 9 (Fig. 5). However, the water quadrats in shade (wild transects) had on average 2.4 species more than quadrats in open water, mainly due to the presence of lemnids.

Most of the first 30 taxa listed, according to the mean coverage per quadrat for managed and wild stretches, were found to differ between the treatment regimes (Figs. 6 and 7). However, both the managed and wild groups included terrace apophytes, mainly found in the upper, mowed quadrats. The first quadrat of the wild transects was mostly mowed too, for the passage. Interestingly, *Agrostis stolonifera* L., which is positioned as the fifth most frequent species ($F = 44\%$) among the dominants of Lake Peipsi, occurred on wild stretches with only a low *F* and coverage. Small terrestrial mosses had a relatively high coverage level on all managed quadrats (Fig. 6).

Species composition of the inlet

During the study period, the coverage of submerged plants in the inlet was estimated to be 70–90%. In 2009–2010, the dominant species were *Ceratophyllum demersum* L. and *Elodea canadensis* Michx. The number of protected species at the water's edge and in the water (*A. gramineum, C. fuscus, Elatine hydropiper* L., *Potamogeton pusillus* L., *P. rutilus* Wolfg.) was highest in the first study in 2006 (Table 4). In 2008 their number has decreased from 5 to 2 because *E. hydropiper, P. pusillus* and *P. rutilus* were not found. The total number of species and the number of declining but not rare species in the inlet did not show any clear trends. Several emergent plants such as *Eleocharis palustris, Glyceria fluitans* (L.) R.Br., *Lythrum salicaria* L., *Phragmites australis, Sium latifolium* L. and *Schoenoplectus lacustris* (L.) Palla appeared within four years of inlet dredging, *i.e.*, since 2008, and have remained in the inlet in following years.

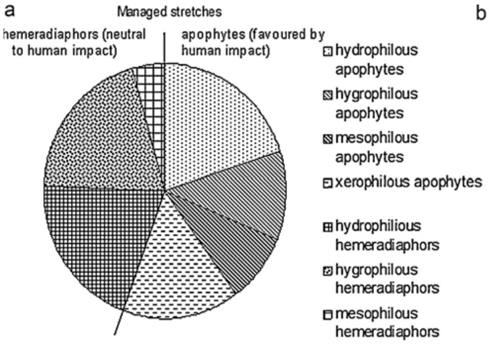

Fig. 4. Ecological division of taxa number on managed and wild shore stretches.

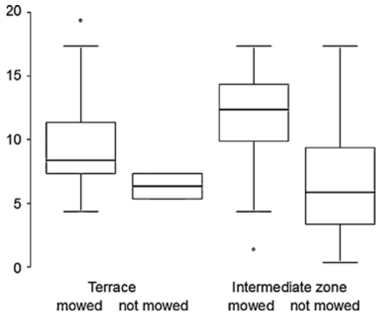

Fig. 5. Average number of taxa per quadrat in terrace and intermediate zones of the managed areas. The middle lines within the boxes indicate median values, boxes indicate 25% and 75% percentiles, whiskers indicate the 1.58 ± interquartile range/n and points stand for the outliers.

Species compositions on differently managed shore stretches

Comparisons based on Jaccard similarity coefficients (JSCs) have revealed a mosaic and inter-annually changing character for the shore and littoral vegetation. Summarizing all species in stretches (properties) studied since 2006 (RA, EL and UUw) for inter-annual comparisons, the JSCs were 0.30–0.50. In comparing all stretches (2006–2008) and/or transects (2009–2010), the maximum values among 462 JSC estimations did not exceed 0.6 and the main portion of JSCs belonged to the 0.10–0.29 interval (Table 5). Clustering the results (Fig. 8), the year and a similar management regime both seemed to have the strongest relationship with higher JSCs, because most of managed transects in 2009 and managed transects in 2010 are placed in different main clusters. More heterogeneous is the third cluster, including all wild areas and most of data from 2006 to 2008. The most obvious reason behind the importance of the year is the changes in water levels. Apophytic mesophytes such as *Trifolium repens* L., *Potentilla anserina* L., *R. repens* L., *Plantago major* L. and *Taraxacum officinale* F.H. Wigg. (coll.) were found only rarely in the 2006–2008 low water years. With rising water levels in 2009–2010 these species became dominant on the moist terraces, and in the same years many wild water quadrats were found to contain lemnids. All these common species increased in a similar manner between 2009 and 2010. We did not find any remarkably lower JSC levels between not-elevated, shortly managed EL and elevated, longer managed RA. However, EL had more species (78) than RA (60), and the numbers of specific species were 22 and 11, respectively. Coverage for 12 species was significantly

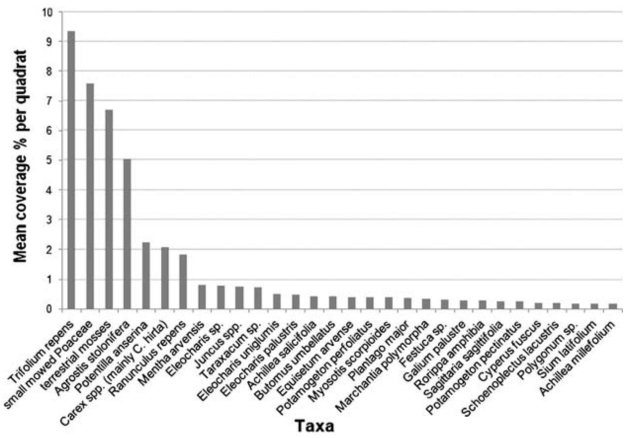

Fig. 6. The first 30 taxa based on the mean C per quadrat in the managed stretches.

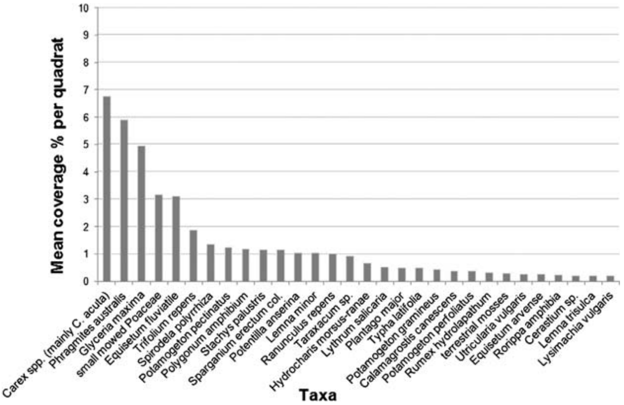

Fig. 7. The first 30 taxa based on the mean C per quadrat in the wild stretches.

higher in EL and for 5 species was higher in RA; hygrophytes were more characteristic in EL. Species richness in the elevated stretches as RA was lower for the lakeshore flora, especially in the dry summers. Comparison of all mowed (78) and not mowed (39) quadrats of managed stretches revealed the favourable impact of mowing on nine apophytes, the small mosses and two hemeradiaphors: *Galium palustre* L. and *Mentha arvensis* L.

An overall comparison between areas under different ownerships, separately for managed and wild stretches, is presented on Fig. 9. The highest species number was found in SL, an area which included a narrow mowed terrace, a less managed intermediate zone and a water zone with the remains of a boat canal, *i.e.*, this area had the most variable microhabitats. The most remarkable increase in species numbers took place in EL which was cleaned in 2006, the year when our study began. Also other longer-studied areas displayed increases in species number, partly for some of the reasons mentioned above. The most uplifted shore areas of JX and VE were clearly richer in species at times with higher water levels.

Discussion

Our results support the assumption that removal of tall emergent plants favours the appearance of small-sized, declining shore species and hydrophytes. For example, *A. gramineum* needs exposed bases (substrate) for reproduction (Moravcová et al. 2001), and the best conditions for seed set are shallow water and recently exposed shores (Hroudová et al. 2004). Also other annuals such as *C. fuscus* need exposed shores for germination. For some tall fen species, shading by *Phragmites* could be not responsible for any reduction in numbers, as it has a pattern of later seasonal growth (Güsewell and Edwards 1999). On the other hand, terraces of managed stretches at Vilusi had very few species in dry periods, and in moist conditions the terrace was inhabited mainly by the commonest, mowing-tolerant apophytes. However, on suitable supralittoral areas on the southern coast of Gulf of Finland associations of *Trifolium repens* and *Potentilla anserina* with other small-sized plants are relatively common also in nature reserves (our unpublished data).

Most important for the richness of the small-sized shore plants are the presence and quality of the intermediate land zone and shallow water. This belt is subjected to the intermediate natural disturbance every year, due to mechanical stress and changing level of the large unregulated water body. Connell (1978) postulates this situation as the most favourable for high species diversity. Despite the fact that the highest number of species was found in the mowed intermediate zone, and also other authors (Güsewell et al. 1998) have revealed higher species richness in mown fen plots than in unmown plots, it is clear that at least some of the declining species cannot tolerate frequent mowing. Seed set remains very scarce or can fail completely, as most of the inflorescences would be cut. There has to be a compromise between mowing to prevent the overgrowth by tall plants and not mowing to favour the growth of smaller declining species, and to determine the best solution is not a task easily solved. Changing water levels seem to be very important for the persistence of macrophyte richness in the managed areas of the lake. In low-water periods there is a large intermediate zone formed for the hygrophytes, but at high water the uniform terrace would be destroyed. However, the high trophy level of the lake is in low-water periods favourable also for reed expansion.

With respect to the inlet, the presence of rare species in the first years after dredging has shown that their decline may have been taking place even before any occupation by tall emergent plants. Submerged species may be suppressed by fast-growing nutrient-demanding (and shading) plants such as *Ceratophyllum* or *Elodea*. Similarly, Thomas et al. (1981) found that floristic diversity in a drainage channel was the highest 1–2 years after dredging. It has been found that submerged macrophytes can start to decline even in the second year after dredging (Wade 1993).

A lakeshore is a naturally disturbed habitat and very probably therefore the number of apophytes (species favoured by disturbed habitats) cannot be clearly associated with management regimes. Another possible reason for the relatively small differences observed in the presence or absence of apophytes between managed and wild may be that the term 'apophyte' when used for species inhabiting water bodies and their shores is not universally understood. Human impact can favour some species directly, by mowing or cutting of reed, but also indirectly, through eutrophication of water bodies. At Vilusi, some apophytes such as *A. stolonifera* grew mainly on the managed areas, and others were mainly on wild stretches, such as nutrient-demanding *Glyceria*, *Spirodela* and *Lemna*.

Our results have revealed the importance of inter-annual variability in floristic composition. Capers (2003), who studied submerged vegetation in a 50 ha tidal freshwater body near the Connecticut River over six years, concluded that, in the face of great

Table 3
Frequency (%) of taxa on wild (F_w) and managed (F_M) shore stretches. In bold: species with statistically significant differences in *F*.

Taxa	F_W	F_M
Agrostis stolonifera	**14**	**82**
Alisma gramineum[a]	14	41
Alisma plantago-aquatica	0	45
Calamagrostis canescens	**43**	**0**
Carex acuta	71	32
Carex hirta	0	41
Ceratophyllum demersum	0	14
Chara contraria	14	50
Cyperus fuscus[a]	14	32
Eleocharis acicularis	0	14
Eleocharis palustris	0	50
Eleocharis spp.	14	41
Eleocharis uniglumis	**0**	**59**
Epilobium hirsutum	0	18
Glyceria maxima	100	27
Hydrocharis morsus-ranae	**57**	**0**
Juncus articulates	0	36
Juncus ranarius	0	18
***Juncus* spp.**	**14**	**82**
Lemna minor	**71**	**5**
Lemna trisulca	**57**	**9**
Lycopus europaeus	0	50
Lysimachia thyrsiflora	**57**	**0**
Lysimachia vulgaris	71	32
Lythrum salicaria	57	18
Marchantia polymorpha	0	23
Mentha arvensis	29	73
Myosotis scorpioides	**14**	**73**
Myosoton aquaticum	0	14
Myriophyllum spicatum	0	45
Phalaris arundinacea	57	32
Phragmites australis	71	36
Poa spp.	0	18
Polygonum spp.	14	32
Potamogeton pectinatus	29	68
Potamogeton perfoliatus	**14**	**82**
Ranunculus reptans	0	32
Rorippa palustris	0	18
Rumex hydrolapathum	**57**	**0**
Rumex maritimus	0	32
Sagina nodosa	0	36
Sagittaria sagittifolia	14	32
Salix seedlings.	0	41
Scolochloa festucacea	43	14
Sium latifolium	0	32
Sonchus spp.	0	34
Spirodela polyrrhiza	**57**	**5**
Stachys palustris	71	32
Zannichellia palustris	0	18
Tussilago farfara	0	18

[a] Protected species.

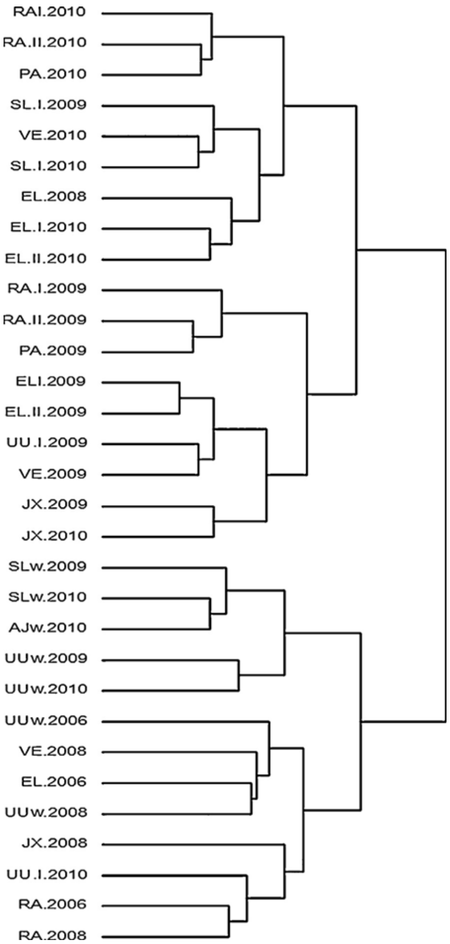

Fig. 8. Shore stretches (from the general studies) and transects clustered by means of Ward's method using Jaccard's similarity coefficients. Wild areas are marked with a *w*. Abbreviations according to Table 2.

small-scale changes observed in the data obtained from quadrates and transects, the persistence of the community in the whole water body was remarkable: JSCs between the years were found to be 0.82–0.94. Our JSC values for the total species in stretches studied every year were half of these values. Obviously, our study area was much smaller, *ca* 1 ha. However, a still more important reason for the differences in these studies may be the positions of the studied habitats, in our case on the border between the shore and water, influenced by yearly (not tidal, 24-hour) changing water levels, changing erosion areas, ice movements, *etc*. In such conditions the impact of the year differences seems to be more or less equal depending upon the type of management regime.

Table 4
The number of macrophyte species in the pond in the different years of the investigation.

Year	Number of protected species	Number of declining species (incl. protected)	Total number of species
2006	5	9	37
2008	1	9	30
2009	0	10	46
2010	2	11	36

Practical conclusion from this work for the remaining species richness is a recommendation for reed removal to a reasonable extent. Besides some macrophytes growing only in reeds, leaving in all the lake parts several larger stands is supporting the birds nesting in the reeds (*Acrocephalus*, *Botaurus*, *Chlidonias*, *Circus*, *Cygnus*, *Locustella*, *Podiceps, etc.*) – there are 64 species inhabiting reed in L. Peipsi (Luigujõe et al. 2008). Reed removal should take place with proven mechanical methods and it is very advisable to leave the surface of the shore and lake bottom uneven, providing variable microhabitats. Reeds and willows removed should be placed far from the water, burned or used otherwise. The importance of mowing is mainly in the avoidance of taller vegetation, because more frequent mowing and leaving the cut hay on the

Table 5
Summary of Jaccard similarity coefficients (JSCs) for shore stretches and transects [M – managed; W – wild].

Similarity range	JSC number	Years included	Characterization of pairs	Exceptions to characteristic pairs
0.50–0.59	2	2009	(a) Lately cleaned transect of EL; (b) uplifted, frequently mowed transects of RA and PA	
0.40–0.49	24	2009, 2010	M transects	SLw and AJw in 2010
0.30–0.39	76	All years	Mainly M transects	SLw and SL M; SLw and M of different owners
0.20–0.29	132	All years	All variants	
0.10–0.19	156	All years	Most of W and M; most of EL2006 and VE2008 together with others	
0.01–0.09	55	All years	Mainly UUw M transect; JX2008 other M and W	
0	17	All years	Mainly UUw2006 and JX2008 with others	

plot is favourable mainly for common lawn species (reproducing by vegetative means), not for the annual species characteristic of open water edges. Some dwarf specimens of rare species such as *C. fuscus* may persist in mowed plots, but their seed production would remain insignificant there. Another factor to consider is that in water bodies with stable (regulated) water levels, artificially formed terraces may be too dry for the smaller-sized lakeshore vegetation. The management regime studied supports the persistence of total species richness in conditions of changing water levels, but probably does not help those species at the stable water edge.

The second practical approach is connected with EU directives. Links between the Water Framework Directive (WFD 2000/60/EC) and Nature Directives (Birds Directive 2009/147/EC and Habitats Directive 92/43/EEC) (2011) declare that for areas summarized as "water-dependent Natura 2000 sites", the objectives of Bird and Habitats Directives (BHD) and WFD apply. Small-sized declining amphibious and shore species, named in this study, are characteristic for water bodies of Natura 3130 type: oligotrophic to mesotrophic standing waters with *Littorelletea uniflorae* and/or *Isoeto-Nanojuncetea*. At the earlier mesotrophic status this type of vegetation was more widely distributed in the studied northern lake part (Mäemets and Mäemets 2001). At continuously rising trophy level scientifically supported management as a tool for keeping this Natura habitat may be artificial, but single possibility, because re-oligotrophication of such large, resilient, transboundary lake is impossible or takes very long time. Processes which have lead to impoverishment of the ecological status have taken place many decades and are probably not reversible, despite demand of WFD to improve ecological quality of lakes very soon (2015).

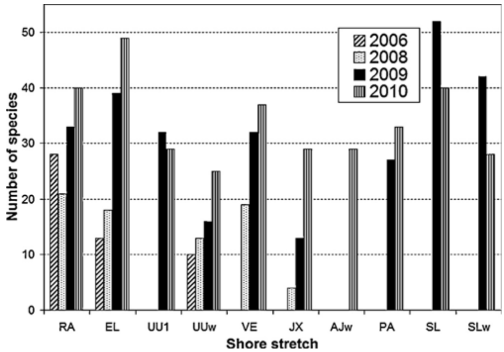

Fig. 9. Total number of taxa for different stretches (Fig. 1, Table 2). Managed and wild (w) areas of the same owner are presented separately (*e.g.*, UU1 and UUw, SL and SLw).

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III

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

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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

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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,

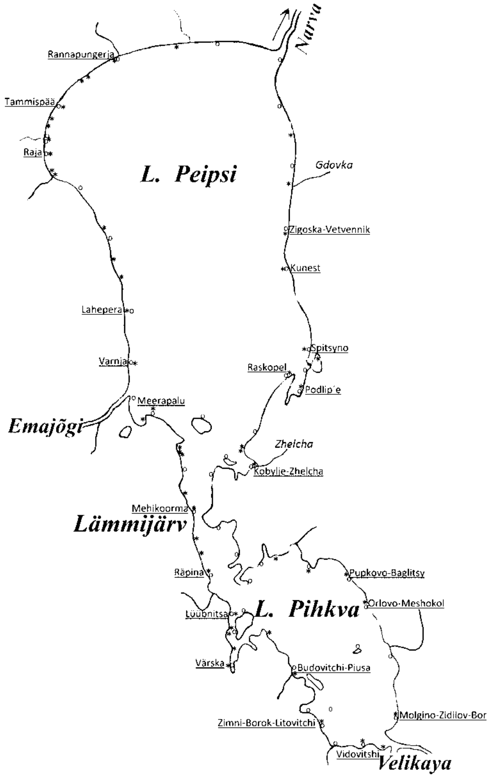

Fig. 1. Location of study stations: o – stations in 1970 and 1980; * – stations in 1997–2014; the names of 22 stations that are best comparable are underlined.

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).

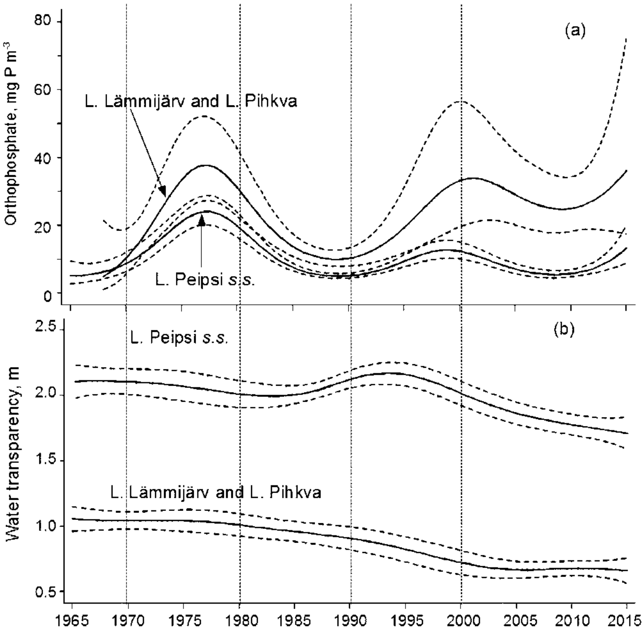

Fig. 2. Predicted mean values with 95% confidence limits of summer ortophosphate concentrations (a) and water transparency (b) in L. Lämmijärv, L. Pihkva, and L. Peipsi *s.s.*

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 *Spirodela*, *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:

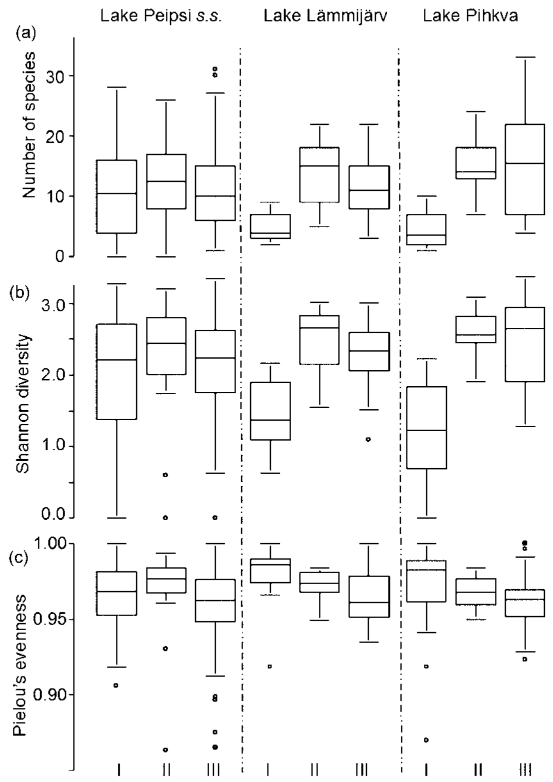

Fig. 3. Average number of macrophyte species per station in different lake parts at different study times (a), Shannon diversity index (b), and Pielou's evenness (c). Boxplots indicate median values and interquartile ranges while whiskers show 5% and 95% quantiles. The Roman numbers: I – 1970; II – 1980;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

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* 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*

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* 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.

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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

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* Number of species was too small for cluster analysis.

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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.

IV

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The response of primary producers to water level
fluctuations and its reflection in ecological assessment.
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The response of primary producers to water level fluctuations and its reflection in ecological assessment

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Abstract. The amplitude of natural fluctuation between annual averages of the water level of Lake Peipsi (3555 km^2) is 1.5 m. A study aimed to examine the impact of water level (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 WL. Changes in littoral phytoplankton were similar with pelagial, with the exclusion of massive wind-caused accumulations of cyanobacteria. At the lowest water increased significantly: a) biomass of phytoplankton and the share of phytoplankton-derived organic carbon in water; b) macrophyte species richness and biomass, including submerged plants and macroalgae. Abundance of epiphytes did not reveal a clear relation with water level. 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 minimum and maximum water level differs at least by one quality class. Remarkably, phytoplankton and large filamentous green algae may yield contrary results from macrophytes: high biomass of phytoplankton and macroalgae at low water simultaneously with species-rich macrovegetation and high biomass of elodeids and charophytes.

Keywords: water level, phytoplankton, macrophytes, epiphytes, biomass, ecological assessment

1. INTRODUCTION

Water bodies are monitored with the aim to evaluate ecological quality based on the response of aquatic bioindicators to the variety of changes. Among the factors controlling the functioning of water ecosystems, the extent, frequency and duration of water level (WL) fluctuations 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), while data on the impact of natural WLF on macrophytes is limited. Furthermore, the 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, 2002).

On the basis of several studies, it was concluded that WLF causes 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 low WL play a role which is similar to anthropogenic eutrophication (Moss et al., 2011). Kangur et al., (2007) found at a sediment study that high temperatures and low WL (especially in spring) resulted in an increased accumulation of organic matter, comparable to eutrophication. Low WL in spring promotes the development of submerged vegetation (Mäemets et al., 2006; Beklioglu et al., 2006). According to Coops and Van Geest (2005) lake-bottom exposure during prolonged low water increased submerged vegetation. In contrast, in the extremely shallow lakes (average depth ≤ 2 m) submerged macrophytes were supported by higher and more stable WL (Cobbaert et al., 2015).

Linking of epiphytes to numerous abiotic and biotic factors complicates the understanding 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 knowledge of phytoplankton biology (Lowe, 1996). Many studies carried out on streams have reported a positive impact of 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 water levels. The effect of WL on the amount of epiphyton 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 herein; Sanchez et al., 2013; Zhang et al., 2015). The position of EP on the host plant, as well as the common top-down control of epiphyton by a fish-macrozoobenthos cascade may outweigh the impact of WL to EP (Jones and Sayer, 2003).

Generalizing data on a very large scale, Wetzel (1992) has 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 outcomes for the whole lake.

Monitoring of unregulated large shallow Lake Peipsi included the years with very different WL: close to the absolute minimum as well as close to the absolute maximum. The observations led to the following hypothesis: low water level 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 km^2, 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´s 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 the 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. WL is unregulated; the amplitude of fluctuation in its annual averages in 1890–2005 was 1.5 m and 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 km^3 and the residence time of water is about two years. The volume of Peipsi at maximum WL (31 m a.s.l.) is 28.91 km^3, and at minimum WL (29 m a.s.l.) 21.57 km^3 (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 highest water levels (Fig. 3). Permanent ice cover usually forms at the beginning of December and lasts in average 118 days (Jaani, 2008). The water is the clearest in June, owing to the low content of phytoplankton in this time. The impact of the waves is remarkable due to the long fetches.

Two major wetland districts are neighbouring Lake Peipsi (Fig. 1). The mires of Peipsi Lowland drain all into the lake and they make up about 40 % of the Estonian part of lowland (Arold, 2005). Extrapolating this percentage to the whole lowland makes about 900 km^2. Alutaguse Lowland drains only partially into Peipsi. In the whole catchment area of Peipsi, wetlands account for 3.4 % (1520 km^2) of the total 44,725 km^2 (Piirimäe et al., 2015).

Data on WL and temperatures for our study were obtained from the Estonian Weather Service of the Estonian Environment Agency. WL measurements were made at the Mustvee Hydrometric Station (58°50′51′′ N, 26°57′04′′ E) on the north-western shore of the lake, 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′s edge showed that the area of reeds (mainly *Phragmites australis*) inside the lake′s borders made up about 1 % of the lake’s area in 2013 (U. Peterson et al., 2014; Report to the Ministry of Environment). It 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 km^2 and constitutes 1.3 % of the lake’s area. This belt area serves as the basis for further calculations. The main submerged plants *Potamogeton perfoliatus, Potamogeton pectinatus, Potamogeton lucens* and *Myriophyllum spicatum* grow mainly 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 km^2 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 the 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 FBM wet weight (Vollenweider et al., 1974) and TOC in average as 33 % of the chemical oxygen demand (Official Journal… 2012/135/EU).

2.3. Littoral data

Field work was carried out annually in the second half of July or in the first half of August 2005–2015, at ten stations in the littoral zone of the lake (Fig. 1). The width of the reed belt was measured with a tapeline. Most reliable data were obtained at the measurements of a narrow stand on the northern shore, not affected by cutting, unlike the stands on the northwest shore. In the southern stations reed stands were wider (100 m or more) and of a changeable shape, not allowing accurate measurements. All macrophyte taxa were recorded on transects (width: 20 m on shore and 10 m in water) starting at the willows or forest by the side of the lake and reaching into the water. Their relative abundances on 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. For the analyse of inter-annual differences in species occurrence, all values of abundance estimations over stations were summarized for every year. Littoral water transparency (SD) was measured from a boat in the deepest part of 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 Chl*a* content on the dominating macrophytes – common reed

(*Phragmites australis*) in the emergent belt; perfoliate pondweed (*Potamogeton perfoliatus*) and spiked milfoil (*Myrophyllum spicatum*) among submerged species. Additionally, in 2012–2015 epiphytic biomass was calculated for the comparison with ADW 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 formaldechyde 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. Although most of the diatoms were identified according to their genus, and only larger diatoms according to their species, it was possible to distinguish an average of 30 diatom taxa per sample. 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 air-dry weight (ADW= air-dry biomass) of macrophytes, epiphyton and phytoplankton, we used published datasets (Mäemets and Freiberg, 2004; Mäemets et al., 2006), reports of Estonian State Monitoring Programme and unpublished datasets of authors, shortly introduced below.

In 1999–2002, a SCUBA-diver conducted sampling of submerged plants at 10 stations; two 0.5 x 0.5 m replicates were taken when plants occurred. This timespan included the highest spring WL in 1999, and the water was at the lowest level (for these sampling years) in spring in 2000 (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 WL (Table 2) into calculations of total hypothetic ADW. Total biomass of epiphyton (see subsection below) on *Potamogeton perfoliatus* (Table 2) was calculated using the extreme values of 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 of the lake: 2.6 m and 1000 g m^{-2}, respectively. These mean values based on 79 samples collected in 2001–2002, and 69 samples in 2012. Extreme averages of 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 % ≈

1:6 as the proportion of biomass inhabited by epiphytes at the extreme water levels. For the sake of simplicity, when calculating the submerged part at the highest WL, we divided the 90 x 1 m reed belt into three 30 m subzones with the following percentage 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.

Values of phytoplankton dry biomass (ADW) in August, the month of maximum FBM in the lake, were calculated for the whole lake, not separately for littoral and pelagial (Table 2). For the biomass of phytoplankton at the lake volume 28.91 km^3 we used FBM in 2010, and at the volume 21.57 km^3, FBM in 2006, according to the volume percentages of the lake parts and averages of FBM in the northern and southern part. ADW was calculated as 20 % of wet biomass and was used for comparison with ADW of submerged plants and algae. Wet biomass of phytoplankton was compared with values in Table 3, for estimation of ecological status for Peipsi (order document N° 44 by Estonian Minister of Environment)

2.5. Statistics

Relationships between the parameters of pelagic water and WL were tested for two different lake parts using generalized linear model (SAS/STAT GENMOD), where the effect of the locations of the sampling stations and seasonality (month) were included. Water variables were log-transformed to meet the assumption of normality. The change in macrophyte abundance and reed width related to change in WL was tested by Spearman correlation analysis and 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). Generalized linear model with repeated measures for the sampling sites (n = 110), was used to estimate the effect of water level on macrophyte abundance. The Poisson distribution was used for macrophyte abundancies 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 pelagial

Significant relationships (Table 4) between the characteristics of pelagic water and WL in 1997–2015 were found for majority of the analysed variables named in section of pelagic data. In the northern, sizable part (Peipsi *s.s.*) 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 FBM at low WL was more pronounced. Remarkably, for this lake part was found also positive correlation between water transparency (SD) and WL, and negative correlation of total phosphorus (TP) with WL (Table 4).

Study period included extreme values of WL: close to the absolute minimum (see Site description) in 2003, 2006–2007 and 2014–2015, and close to the absolute maximum in 1999 and 2010-2011 (Fig. 2). Comparison of the data of these two groups for the whole lake revealed that average CNR (°) in May-August of high-water years (mean ± St.error): 81.9 ± 3.01 (n = 68) was more than two times higher than in the years of the lowest WL: 36.4 ± 1.42 (n = 128). Remarkably, this increase of CNR was not connected with significant increase in chemical oxygen demand by dichromatic consumption (CODCr) at high-water: 34.2 ± 1.42 ; at low water 30.6 ± 0.84 mg O L^{-1}). At low water 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 in Methods) increased with the decreasing WL (Fig.4).

Comparison of SD between the littoral and the pelagial for 2005–2015 showed that its values at sampling time were lower in the littoral: 0.96 ± 0.04 m *versus* 1.25 ± 0.05 m in the pelagial (t-test $p < 0.001$, $n = 69$). Similarly to the pelgial of the shallow Lämmijärv, SD of the littoral had a positive correlation with 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 WL (Fig. 5). Large filamentous green algae *Cladophora* (dominant), *Spirogyra*, *Mougeotia*, *Ulothrix*, *Chaetophora*, *Zygnema, etc*. were markedly supported by low WL ($r = -0.71$). Besides the increase in total species number (including shore plants and helophytes) at retreating water, the number of submerged species was also significantly ($r = -0.82$) higher at low WL. Shallow water in spring was most favourable for *Potamogeton perfoliatus* ($r = -0.81$), *Myriophyllum spicatum* ($r = -0.76$), *Potamogeton pectinatus* ($r = -0.74$) and *Chara contraria* ($r = -0.65$). Results of modelling predicted a 1.6…4-time increase in the abundance of these species at a 1 m decrease in water level (Table 5). Moreover, low water was favourable for two rare, protected species: amphibious *Alisma gramineum* ($r = -0.53$), and hygrophilous *Cyperus fuscus.* Nutrient-demanding *Lemna gibba* and *Zannichellia palustris* occurred more frequently at low WL. Despite high temperatures at high WL in 2010 (Fig. 5a) the occurrence of any of the aforementioned taxa was not enhanced.

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 stand displayed remarkable oscillations (Fig. 6), but was not significantly correlated with 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 WL.

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 the growing depth of submerged plants 0.1–3.5 m (for 90 % 0.2–1.9 m). When 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* ($r = -0.18$, $p = 0.046$), while it was lacking for *Myriophyllum.* The percentage of diatoms in 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 total number of species decreased with depth. Irrespective of this relationship, 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 (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 dynamics of 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* constituted the main share 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 (Fig. 8).

The influence of WL on 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 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 water level 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 ADW of the submerged reed shoots at high WL yielded 23.1 kg per 1 m wide transect of the 90 m reed belt. For the lowest WL, ADW of submerged reed was calculated as 1/6 and it was about 3.7 kg for transect.

In Lake Peipsi phytoplankton dominated over the ADW of submerged plants and epiphytes (Table 7). Interestingly, the ratios of biomasses at the lowest to the highest water level: 2.2 for *Potamogeton* spp. and 2.6 for phytoplankton were similar. Regarding the FBM (mean±St.error for growing period), ecological status of Peipsi according to the Water Framework Directive (order document N° 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, according to the high abundance of filamentous 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 with the years 2000 and 1999 (Tables 2 and 7).

4. DISCUSSION

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 prevailing group, the difference of ADW of these two submerged producers at extreme water levels may be similar. Thereat, it is probable that in boreal lakes of lower trophy level extreme ADW differs within lesser amplitude. In Peipsi, the twofold difference in easily degradable biomass (algae and/or submerged plants) must have remarkable influence on the heterotrophic part of the food web. Our results are in accordance with the statements that WLF causes 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 food web is under government of WL *via* resuspension, turbidity and productivity. The recent studies in Peipsi showed an increase in internal phosphorus loading with decreased WL, whereby CY biomass in August positively correlated with this loading (Tammeorg et al., 2016). Low water level creates favourable conditions for sediment resuspension that results in decreased water transparency *via* increased concentrations of suspended solids and phytoplankton. Increased resuspension and phosphorus loading at low WL has been found also in large, extremely shallow Lake Võrtsjärv (Nõges and Nõges, 1998). Despite the decline of transparency at low WL, 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) has suggested that larger temperature fluctuations and light pulses at low WL, especially in spring, stimulate the germination of propagules. Similarly, Lombardo (2005) highlighted the importance of spring light conditions. The light favours significantly germination of *Chara* oospores, since it activates cytochromes (Takatori and Imahori, 1971). During the period of our study, the best year for *Chara contraria* was 2006, when WL was very low already in spring (Figures 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 WL, while FBM (particularly CY) was also influenced by water temperature. Besides WL, extraordinary weather conditions may also trigger long-term shifts in the plankton community in the following seasons. A steep decline in pelagic FBM in 2008 followed the ice-free winter of that year. This 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 the impact of the WL may be more delayed than in smaller water bodies (cf. Beaulieu et al., 2013). The amount and composition of littoral phytoplankton depends to the large extent on the prevalent direction of the wind at the sampling, while 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 WL. 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 change in redox status (Kalin and Smith, 2007). For the reeds, the impacts of other, more accidental factors, *e.g.* 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 low WL would enhance their growth was not verified. The effect of 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 lowest (2006) as well as at highest WL (2010), long-lasting high temperature apparently overcame negative impact of 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 WL was moderated by mechanical stress. The amount of EP in relation to growing depth varied mostly on *Potamogeton* and least on *Phragmites*, because the range of variability of the latter's growing depth was narrower.

Allochthonous and autochthonous organic matter

According to Wantzen et al. (2008), 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 CO_2 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 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 intense aeration and mineralization of all organic matter at low WL. The decomposition and mineralization at retreating WL promotes a new rise in 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 WL.

The "brownification" (cf Graneli, 2012; Kritzberg et al., 2012) of Peipsi seems to be a periodic WL-driven fluctuation. The rising of CNR but not CODCr at high WL probably results from refractory character of allochthonous organic matter in comparison with autochthonous. Remembering Wetzel (1992), decomposition of dissolved organic matter from wetland and littoral is slow. In comparison, FBM had a positive correlation with CODCr at different WL, but the relative importance of phytoplankton in total organic carbon increased during the years of 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 abundance of the lake´s producers at high WL.

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. It 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 filamentous algae, considered good indicators in the lakes under hydrological pressures and with 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 WL and cause poorer estimation of the ecological status. Low water is favorable for nutrient-demanding hydrophytes as *Lemna gibba* and *Zannichellia palustris*. In contrary, low water enhances macrophytes indicative for good status. In temporal habitats available due to retreating water, occur species which are declining due to eutrophication and overgrowing littoral (*Cyperus fuscus* and *Alisma gramineum*). Increase in submerged species and in total species richness - indictors of good status - also took place at low WL. Thus, the estimations of lake status according to different groups of biota may yield different estimations.

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. However, besides this positive impact of low WL on macrophyte species richness, concurrently is enhanced overgrowth of shallow slopes by tall plants (reeds) and “centrifugal” distribution of species: tall productive plants occupy the main, largest part of habitat and small-sized plants (*incl. Alisma* and *Cyperus*) are pushed to peripheral areas (Keddy, 2010). The effect of high-water years on reeds seems to have also two-pronged effect. In our study reed stand in the shallowest water was more successful in high-water periods but in initially deeper growth areas reeds declined in these years. By Vretare et al. (2001) *Phragmites* in deeper waters allocated less resources to its below-ground part and was therefore more sensitive to uprooting. Rising water reduces the supply rate of oxygen to the submerged parts by increasing path to the rhizomes (Deegan et al., 2007).

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Figure captions

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 (names).

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

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

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

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

Fig. 6. Width of the reed belt at Rannapungerja (northern coast) and water level (average of May–July). Reed width was not measured in 2008.

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

Fig. 8. Phytoplankton biomass (**NB! not Chlorophyll!**) 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 they are presented at the bottom of the graph: ellipse – *Anabaena*; rectangle – *Gloeotrichia.* n = 110.

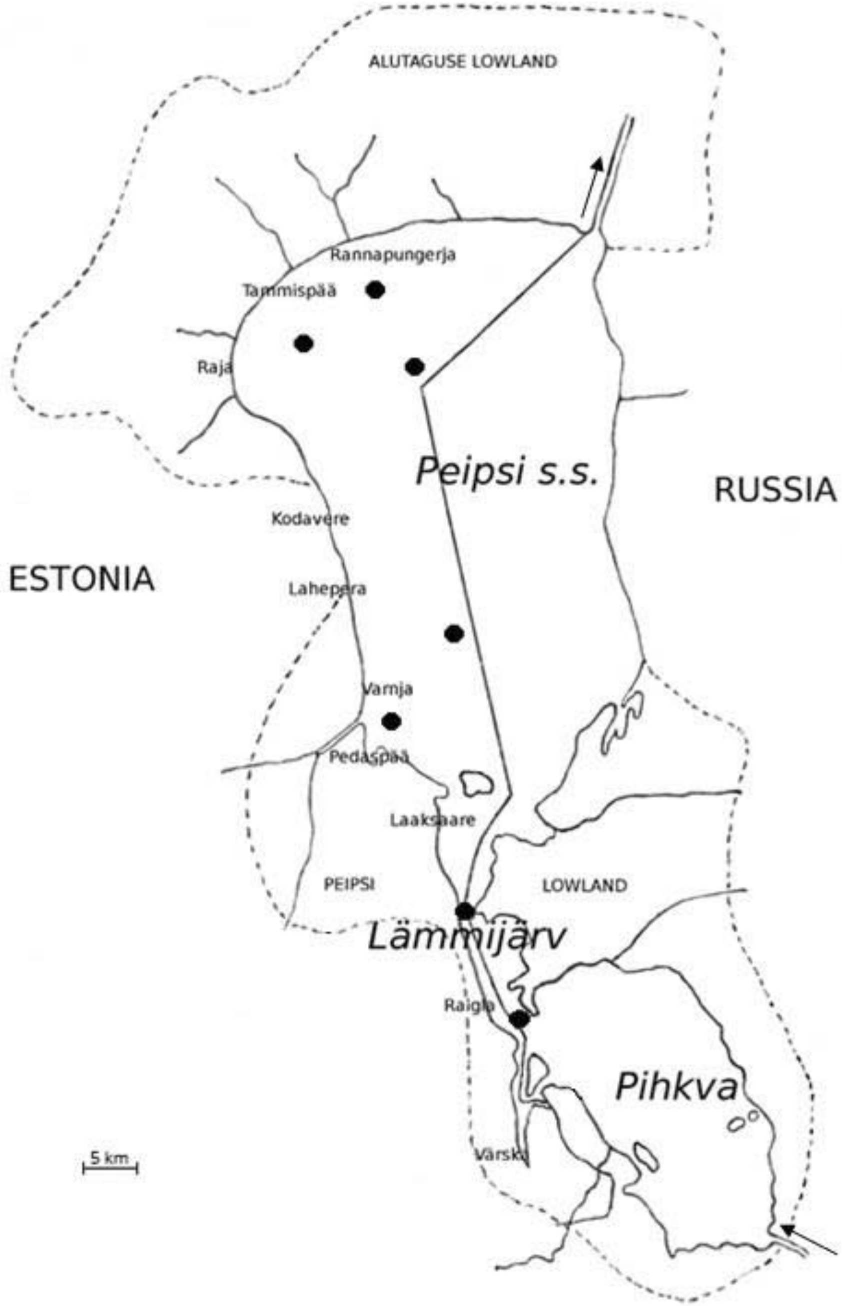
ALUTAGUSE LOWLAND
Rannapungerja
Tammispää
Raja
Peipsi s.s.
RUSSIA
Kodavere
ESTONIA
Lahepera
Varnja
Pedaspää
Laaksaare
PEIPSI
LOWLAND
Lämmijärv
Raigla
Pihkva
Värska
5 km

Fig. 1.

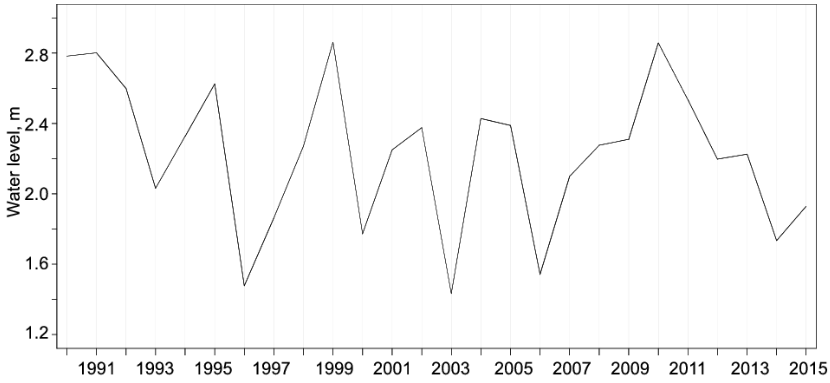

Fig. 2.

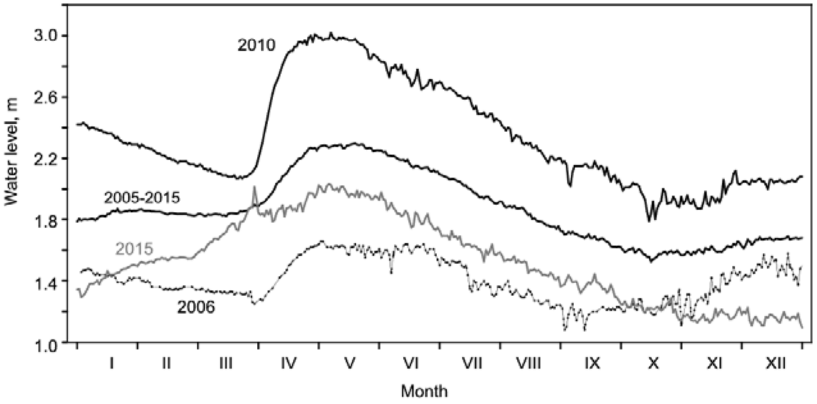

Fig. 3.

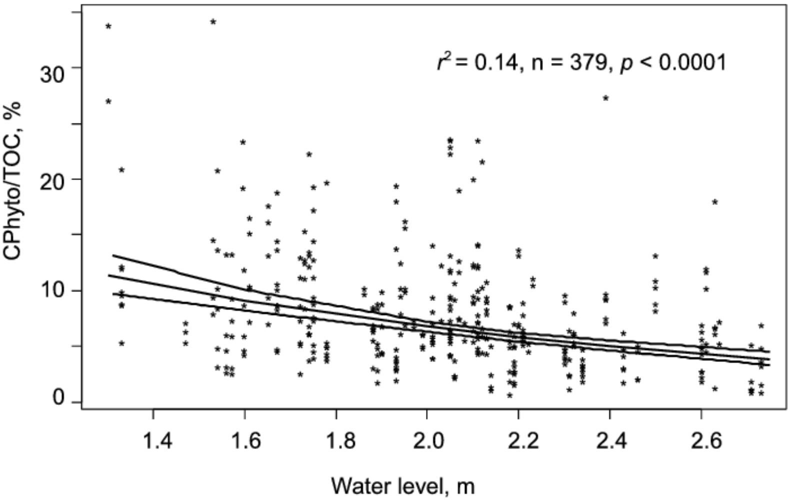

Fig. 4.

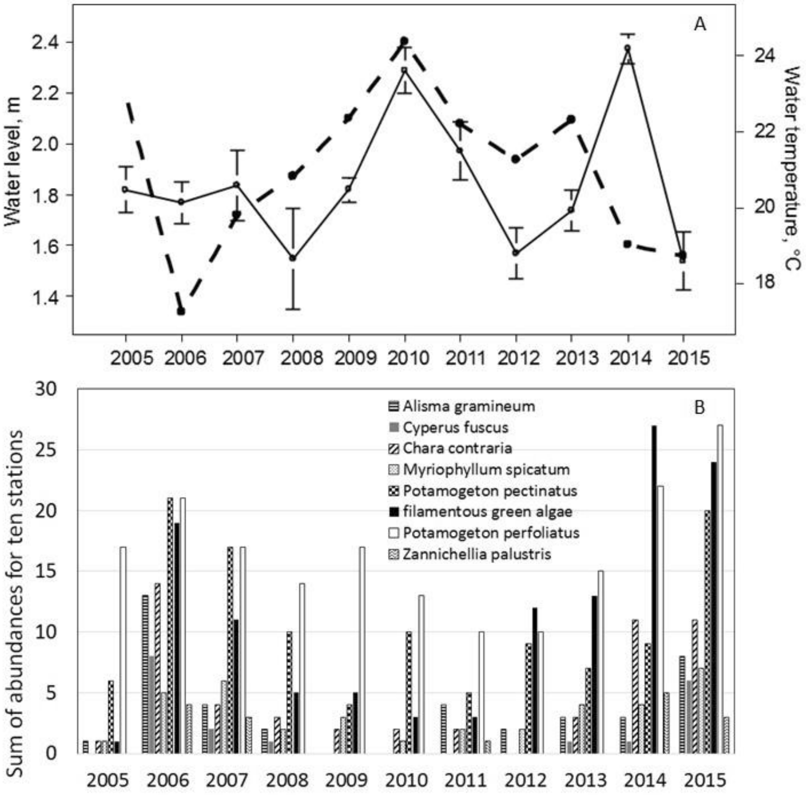
A
Water level, m
2.4
2.2
2.0
1.8
1.6
1.4
Water temperature, °C
24
22
20
18
2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
B
Sum of abundances for ten stations
30
25
20
15
10
5
0
Alisma gramineum
Cyperus fuscus
Chara contraria
Myriophyllum spicatum
Potamogeton pectinatus
filamentous green algae
Potamogeton perfoliatus
Zannichellia palustris
2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015

Fig. 5.

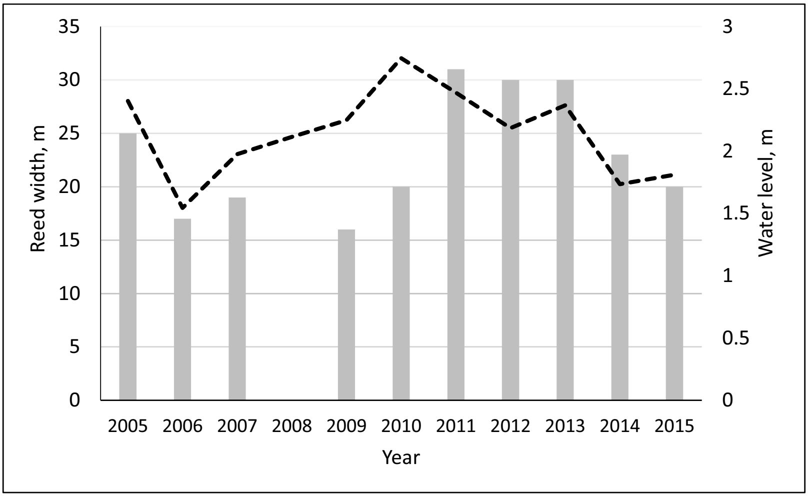
35
30
25
20
15
10
5
0
Reed width, m
3
2.5
2
1.5
1
0.5
0
Water level, m
2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
Year

Fig. 6.

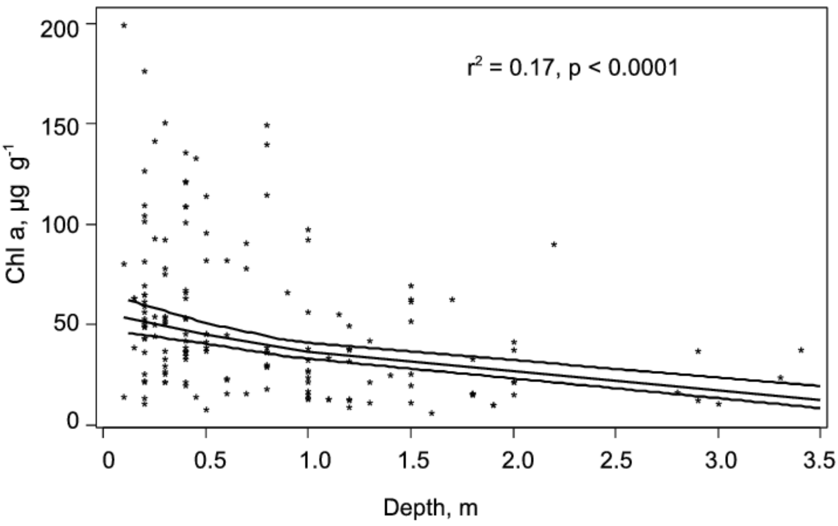
$r^2 = 0.17$, $p < 0.0001$
Chl a, µg g⁻¹
200
150
100
50
0
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Depth, m

Fig. 7.

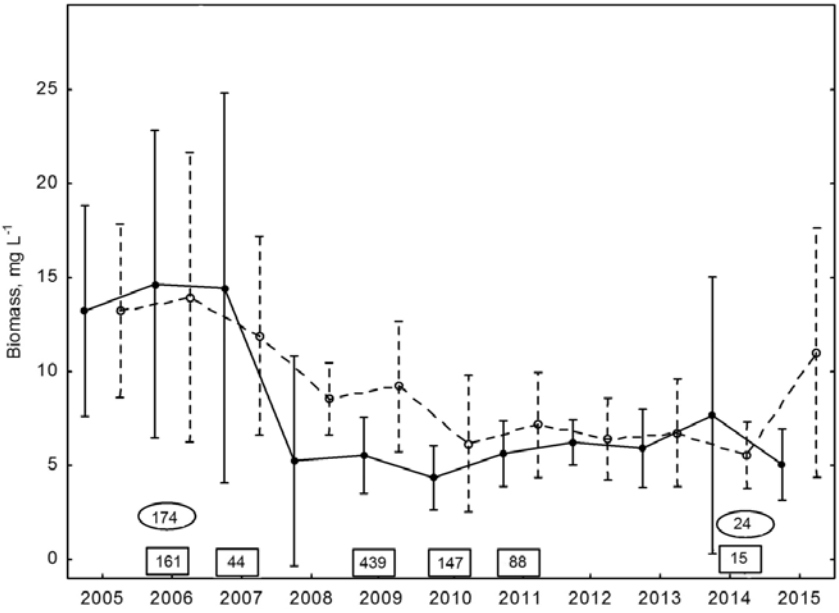
Biomass, mg L⁻¹
25
20
15
10
5
0
174
24
161
44
439
147
88
15
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015

Fig. 8.

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

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

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

PRODUCER	Maximum WL average ADW	Minimum WL average ADW	Overall mean ADW
Phragmites australis, shoots, g m^{-2}			1000
Potamogeton perfoliatus, shoots, g m^{-2}	23.3 (1999)	48.4 (2000)	
Potamogeton pectinatus, shoots, g m^{-2}	0.8 (1999)	4.6 (2000)	
Epiphytes on *Phragmites*, mg g^{-1}			0.55
Epiphytes on *P. perfoliatus*, 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)	

Table 3. Values of phytoplankton (wet) biomass (FBM) and abundance of large filamentous green algae used for the assessment of ecological status of Lake Peipsi according to the Water Framework Directive (adapted from order document N° 44 by Estonian Minister of Environment)

Indicator	Lake part	High	Good	Moderate	Poor	Bad
FBM (April–October) mg/l	Peipsi *s.s.*	≤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		0	1	2–3	4	5

Table 4. Estimated change (increase in bold) with confidence limits of pelagic water characteristics at 1 m decrease of water level for the 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 *s.s.* (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

Table 5. The 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

Variables	Results of GENMOD n = 110	
	Estimated ratio with conf. 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
Potamogeton perfoliatus	1.6 (1.1–2.1)	0.03
Potamogeton pectinatus	2.5 (1.5–4)	0.026
Myriophyllum spicatum	3.4 (1.7–6)	0.01
Chara contraria	4 (1.6–10)	0.038
Large filamentous algae	3.1 (1.7–5)	0.014

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

Variables	Unit	Valid n	Mean	Lower quartile	Upper quartile	Std.Dev.	Std. error
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 *Myriophyllum*	µg g^{-1}	36	84.00	45.60	110.11	60.4	8.77
Chl*a* EP *Phragmites*	µg g^{-1}	118	13.00	6.66	16.07	10.7	0.98
Chl*a* EP *Potamogeton*	µg g^{-1}	157	50.44	23.00	64.06	37.3	2.97
EP bm *Myriophyllum*	mg g^{-1}	20	2.88	1,40	3.59	2.39	0.54
EP bm *Phragmites*	mg g^{-1}	52	0.55	0.20	0.48	1.38	0.19
EP bm *Potamogeton*	mg g^{-1}	65	1.96	1.13	2.53	1.25	0.16

Table 7. Differences in biomass of the main primary producers in Lake Peipsi at extreme water levels, 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 minim. WL	ADW (t) at maxim. WL
Submerged part of *Phragmites* shoots, available for epiphyton	1 932	12 063
Epiphytes on *Phragmites*	1.1	6.6
Shoots of *Potamogeton perfoliatus* + *P. pectinatus*	530	241
Epiphytes on *Potamogeton perfoliatus*	1.2	0.5
Large filamentous algae*	185	≈0
Phytoplankton of the whole lake (pelagial+littoral) in August	69 065	26 156

*Calculated only for the 20 m belt

Primaarprodutsentide sõltuvus veetaseme kõikumisest ning selle kajastumine veekogu ökoloogilise seisundi hinnangus

Helle Mäemets, Reet Laugaste, Kadi Palmik ja Marina Haldna

Peipsi järve (pindala 3555 km^2) veetase on väga muutlik: aasta keskmiste väärtuste erinevus küünib 1,5 meetrini. Veetaseme kõikumiste mõju fütoplanktonile, makrofüütidele (suurtaimedele) ja epifüütonile (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 sarnased, välja arvatud tuule mõjul akumuleeruvate tsüanobakterite (sinivetikate) suurem hulk litoraalis veeõitsengute ajal. Võrreldes maksimum- ja miinimumveetasemega aastaid, leiti, et madalaima veeseisu korral tõusid oluliselt: a) fütoplanktoni biomass ja selle osatähtsus vee orgaanilise süsiniku sisalduses; b) suurtaimede liigirikkus ja biomass, sealhulgas veesiseste taimede ja makrovetikate oma. Epifüütide rohkuses ei ilmnenud olulist seost veetasemega. 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 tõuseb 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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Mäemets, H., **Palmik, K.** & Haldna, M. 2016. Eutrophication-driven spatial and temporal changes in macrophyte diversity in Lake Peipsi. *Proceedings of the Estonian Academy of Sciences* **65**: 394–407.

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Popular-scientific publications

Mäemets, H., Freiberg, L., **Palmik, K**., Sudnitsõna, D. & Kozõreva, K. 2008. Suurtaimestik. Haberman, J., Timm, T., Raukas, A. (Eds.). Peipsi (227−240). Tartu: Eesti Loodusfoto.

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Participation in international conferences:

The 12th European Weed Research Society Symposium: Aquatic Weeds, Jyväskylä, Finland, August 24–28, 2009. Oral presentation: Palmik, K. & Mäemets, H. Species richness on differently managed shore stretches of Lake Peipsi, Estonia.

Symposium The Role of Littoral Processes in Lake Ecology, Hegne, Germany, January 29–31, 2010. Oral presentation: Palmik, K., Haldna, M. & Mäemets, H. Impact of water level fluctuations on macrophyte characteristics in Lake Peipsi.

The 7th International Shallow Lake Conference, Wuxi, China, April 24–28, 2011. Poster presentation: Palmik, K., Mäemets, H. & Haldna, M. The floristic composition of the managed shore areas of Lake Peipsi, Estonia.

The 7th Symposium for European Freshwater Sciences, SEFS 7, Girona, Spain, June 6th–July 1st, 2011. Poster presentation: Palmik, K., Mäemets, H. & Haldna, M. Impact of water level fluctuations on macrophytes in Lake Peipsi.

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„8th International School of Conservation Biology“, Rovinj, Croatia, June 23rd–July 1st, 2012.

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Peamiste publikatsioonide loetelu:

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

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Populaarteaduslikud tööd:

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